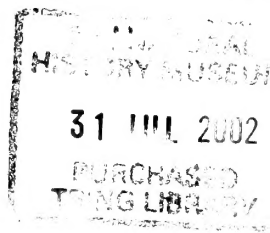


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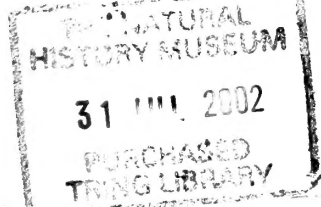
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From Japan through Asia to the world: building bridges in ornithological science

On behalf of the Ornithological Society of Japan, I would like to express my great pleasure at the publication of this first edition of *Ornithological Science*. This is an international peer-reviewed journal that will be published twice yearly. The purposes of the journal are to promote ornithological studies in Japan and other Asian countries, and to facilitate the exchange of information between ornithological scientists working both inside and outside Asia.

In Japan, China, Korea, and many other Asian countries, both the amount and importance of ornithological research are increasing. Research in Asia encompasses areas of ornithological science that have emerged relatively recently, including the behavioral ecology, conservation biology and molecular phylogenetics of birds, as well as more traditional fields such as bird distribution, population and community ecology and dynamics, and physiology. However, often the results of ornithological research carried out in Asia have been published in domestic journals solely in Asian languages. Although the work may be of high quality and great importance, language barriers and difficulty acquiring published materials can prevent foreign scientists accessing and understanding the research done by their colleagues. We would like to help remove these difficulties with the publication of *Ornithological Science*.

In Asia, there are so many interesting birds and subjects for research. Although we know that the amount of research being done in this region is increasing, we believe that many interesting and important studies of Asian avifauna remain unpublished. As a venue for the publication of original ornithological research, *Ornithological Science* is open to all scientists, and there are advantages to publishing within its pages, as described on the reverse of the front cover and in the editorial of this edition. The publication and dissemination of interesting work encourages further study, for example, by scientists extending research to other species and groups of birds. We hope that *Ornithological Science* will facilitate the development of ornithological research in this way.

As well as publishing original research, the editors of *Ornithological Science* would like to encourage scientists to contribute review papers on particular topics, to promote the understanding of different fields of research. Examples of topics for review could include the origin and evolution of birds endemic to Asia, mate selection and social structure of Asian birds e.g. babblers and pheasants, the present status and conservation of endangered birds in Asia, the use of molecular data for ecological bird studies, the use of GIS (Geographic Information Systems) for habitat and distribution analyses, and modern technologies used in migration studies. Producing reviews in a common language, based on previous publications in scientists' native languages, should give a better perspective on the state of research in various fields of Asian ornithology.

The avifaunas of different countries are, or used to be, connected to each other. Bird species of one area were differentiated from those occupying neighboring areas. Migratory birds move over a number of different countries. Therefore, in order to study the origin, distribution, ecology, migration and conservation of birds, international cooperation and collaboration are very important. During the last ten years, I have enjoyed collaborating with Korean, Chinese, Indian, Russian, and American ornithologists to satellite-track the migration of cranes, swans and storks. We have obtained an enormous amount of valuable data on the migration routes, migration patterns through time, relative importance of resting sites, and habitat characteristics of important sites. Our studies have resulted in various conservation activities relevant to these birds and their habitats. Through my involvement with this research, I realized that international cooperation and collaboration are extremely important. My colleagues and I have already published many papers in various academic journals, but this attractive new ornithological journal is appealing to us as a publication venue, and we are looking forward to presenting our work within its pages. I would like to encourage collaborative research groups, e.g. Asian research groups studying geese, swans, egrets and raptors, to publish their results here. Publishing the results of joint work in international journals like *Ornithological Science* should help broaden the scope of our research

activities, and increase the depth of our friendships.

This year, the Ornithological Society of Japan will celebrate its 90th anniversary. We now have about 1,200 members, and this number is increasing. Most members of the Society are Japanese. However, we encourage new members from many countries to join, particularly ornithological scientists working in Asian countries. We would like to broaden our research horizons, while forming as many friendships and collaborative working relationships as possible. With the publication of Ornithological Science, the Ornithological Society of Japan will enter into a new generation of its history. Ornithology in Japan, and ornithologists working there, will benefit from their area of interest and expertise becoming more open. This will facilitate an increasing level of connection with other ornithological scientists in Asia and around the world. Japan is a beautiful country with a diverse landscape including forests, mountains and islands, and has a lot of interesting areas for ornithological studies. It is my great pleasure to welcome visitors to our country to study birds, and also to enjoy birds through subscribing to Ornithological Science.

I sincerely hope that Ornithological Science will help build bridges connecting ornithological scientists from different countries.

January 4, 2002

Hiroyoshi HIGUCHI

President of the Ornithological Society of Japan

“Ornithological Science”, the new English publication from Japan

Ornithological Science has evolved from the Japanese Journal of Ornithology, which was composed of both English and Japanese papers and was published four issues; numbers 50 volumes last year. Twenty-five years ago, when I joined the society, many papers were written in Japanese. However, in recent years most of them are written in English. This marked a great change in our society and an outstanding growth in a new generation of Japanese ornithologists. We felt now was a good opportunity to divide the journal into two parts: English and Japanese. This is the first issue of the English addition.

Ornithological Science will be published twice a year. It includes special features, original articles, reviews, short communications, and commentaries on all aspects of ornithology. All papers will be critically reviewed by at least two referees. If accepted, submissions will be published in a high quality format without a long delay.

I hope that this new journal will have be of international caliber and will contain high quality papers of ornithology from not only Japan but also other Eastern and/or South-Eastern Asian nations. Of course, we would be glad to receive papers from other parts of the world. In keeping with our aims, we have invited powerful Advisory Board members from Asian, European, Australian, and North American countries listed on the back cover.

We welcome your support as authors, readers, referees, and subscribers.

Keisuke UEDA
Editor-in-Chief

SPECIAL FEATURE

Interspecific segregation and attraction in forest birds

INTRODUCTION

How different species coexist in a given habitat or in a given area is one of the central questions in community ecology. During the 1960s and 1970s, MacArthur's niche theory provided a scientific basis for researchers approaching this subject. Niche theory is founded on two basic assumptions: Interspecific competition is an organizing force affecting communities and environments are at equilibrium determined by resource limitation. Because forest birds appeared clearly to fulfil these assumptions, many studies demonstrated their interspecific differences in resource use based on niche theory. Niche differences were often interpreted as the result of interspecific competition for limited resources under equilibrium conditions; yet, hardly any of these studies questioned the intrinsic assumptions of niche theory. Meanwhile, other factors, such as predation, mutualism, disturbance and chance had begun to be focused on as alternative processes affecting community organization. Doubts and criticisms of MacArthur's paradigm resulted in considerable controversy over community organization during the 1980s.

During the 1990s, the approach to biotic communities has become pluralistic. Interspecific competition is now seen as one of several forces organizing communities and resource equilibrium is seen as one of several environmental conditions. When we study how forest birds coexist, we may begin therefore with three questions: firstly, we may ask what kind of segregation is most important and how does it differ among target species. Secondly, we may ask what kind of interspecific interaction is most effective for coexistence. The interaction may be negative, such as competition or predation, or positive, such as mutualism or commensalism. Thirdly, we may ask how interspecific interactions change as environmental conditions vary. In particular, the dynamics of resource abundance and distribution must be examined in order to solve the equilibrium problem.

This special feature is composed of three parts: (1) segregation mechanisms, (2) attraction mechanisms and (3) the effect of food distribution. The first two papers, from Australia, focus on the segregation mechanisms of forest birds. Loyn reviews the pattern of ecological distribution of forest birds in southeastern Australia by examining the incidences of range overlap among congeneric species and mechanisms segregating them. From this broad-scale approach, he confirms that habitat difference is the primary segregation mechanism, and that differences in foraging stratum or substrate are most important for coexistence in the same habitat. As a unique feature of the Australian eucalypt forest environment, Loyn indicates that the indiscriminate interspecific aggression of some communal-breeding species has decreased not only the bird species diversity but also the ecosystem health in forests. Recher and his colleagues compare the foraging ecology of five ground-pouncing birds (Australian robins) in woodlands in western Australia. Ecological segregation among understory-foraging birds has been much less studied than among canopy-foraging birds owing to the simpler structure of foraging substrates. Recher et al. found some fine-scale segregation among species by considering the mosaic of available ground substrates, but recognized that foraging ecology was more similar among different species in the same habitat than among conspecific individuals in different habitats. Loyn's and Recher et al.'s papers indicate that a broader range of species or habitats should be analyzed when studying ecological segregation.

The third and fourth papers focus on attraction mechanisms or positive interactions between species, which have rarely been considered in studies of forest bird communities. Mönkkönen and Forsman review their own original studies on heterospecific attraction, that is, a habitat selection process where colonizing individuals (migrants) use the presence of other species (residents) as cues to profitable breeding sites in relation to food availability or predation risk. From biogeographical, theoretical and experimental studies in Fennoscandia and North America, they conclude that heterospecific attraction is a common and widespread process resulting in high species diversity among forest birds particularly in seasonal environments. Mixed-species flocking is another positive interaction in forest birds. Seki and Sato report that different bird species increase the overlap of

the foraging sites they use and the food they eat by frequent participation in mixed-flocks in the winter following an extremely severe typhoon. Seki and Sato consider interspecific attraction to be a result of increased predation risk following reduction in vegetation cover, but not of decreased food abundance. These two studies indicate the importance of specifying what environmental conditions facilitate a positive interaction over a negative one.

The remaining four papers all pertain to the effects of food-supply on forest birds. The three papers from Japan demonstrate how the abundance and distribution of prey influence the substrate-use difference among canopy-foraging insectivorous birds. Murakami examines how birds respond to the drastic distributional changes of Lepidoptera larvae, which migrate from the canopy to the forest floor. He finds two different responses: some species change their foraging height in parallel with the changing distribution of Lepidoptera larvae, while others switch to different prey without altering their foraging height. Mizutani and Hijii reveal that two closely related and similar-sized species of birds (Parus) differentiated between foraging trees according to their prey-size preference, determined by whether they were single- or multiple-prey loaders. Hino and his colleagues also find interspecifically different use of tree species among Parus, but they relate it to the birds' prey-searching techniques. These three studies indicate that forest-substrate segregation between closely related species can be related to species-specific foraging tactics without considering interspecific competition. Sodhi's paper is the only contribution from tropical forests in this special feature. He reviews the few, but interesting, studies on the effects of food-supply on forest bird ecology in Southeast Asia. Further challenging surveys are expected to be conducted in this region where a range of fascinating phenomena, such as El Nino, mass flowering or fruiting, and year-round mixed-species flocking, occur.

Lastly, we must emphasize that the findings from studies on interspecific interactions and/or food resource distribution affecting species coexistence have significant implications for bird conservation. For example, the numerical changes of some bird species caused by habitat loss or fragmentation decrease overall species diversity through interspecific aggression or attraction. The different responses of birds to varying prey distribution among different tree species demonstrates that tree species composition is an important habitat factor affecting the diversity of canopy-foraging bird species in forests. The mosaic complexity of ground substrates may be an equally significant factor for ground-pouncing birds.

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Patterns of ecological segregation among forest and woodland birds in south-eastern Australia

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Abstract Much information has been gathered on birds of eucalypt forests and woodlands in south-eastern Australia. This was examined to assess some of the mechanisms of ecological segregation that may apply. A database was constructed of 209 species pairs (148 species from 48 genera). Most patterns resemble those reported overseas, with habitat and range featuring as major segregating mechanisms. Use of different strata and substrates was the dominant primary mechanism allowing use of identical space by congeners. Mechanisms such as specific food preferences, migration and choice of nest sites contributed but rarely as primary factors. One species pair appears to show no ecological segregation, despite co-existence in varying proportions over a large geographical range. Indiscriminate interspecific aggression is used by some species to maintain high levels of resources for themselves, in environments that can sustain such resources throughout the year. Communal breeding is a feature of those species. Implications for conservation are discussed.

Key words Birds, Co-existence, Ecological segregation, Eucalypts, Forests, Habitat

Two of the central questions that ecologists endeavour to address concern the number of species that can co-exist in a given habitat or area, and the mechanisms they have evolved to facilitate co-existence (Lack 1971). The questions are of theoretical interest in understanding adaptive radiation and the origin of species (Darwin 1859; Cody 1974; Quammen 1996). They are also of practical interest in our attempts to conserve species in areas of protected habitat that are typically diminished in area, isolated from other reserves and subject to a range of human pressures and threatening processes (May 1978; Diamond 1981; Tilman 1982). It is of special interest to examine these questions in Australia, where both the environment and the bird fauna have many unique features (Ford 1989).

When Lack (1971) presented his global analysis of ecological isolation in birds, much remained to be learned about the basic natural history and ecology of Australian forest birds. Since that time, great advances have been made by professional and amateur biologists, building on the pioneering studies such as

those by Keast (1957, 1968), Kikkawa (1968) and Kikkawa and Pearse (1969). Some studies have focused on ecology of particular species and groups (Ford 1985), while others have examined whole bird communities (Recher 1985). The amateur bird-watching community has grown and its energy has been harnessed to provide distributional data in two national Atlas projects (Blakers et al. 1984; Barrett et al. in prep.), the first attempted on a continental scale. Regional Atlases have been published using these and other data sets (e.g. Emison et al. 1987; Cooper & McAllan 1995). A temporal monitoring project (the Australian Bird Count) has been used with Atlas data to provide new insights on seasonal movements (Clarke et al. 1999; Griffioen 2001). Excellent ecological texts on birds have been published by Rowley (1974), Serventy and Whittell (1976), Keast et al. (1985) and Ford (1989). Data to help conserve threatened taxa have been compiled in an action plan (Garnett & Crowley 2000). Five volumes have been completed for a seven-volume Handbook of Birds of Australia, New Zealand and Antarctica (Marchant & Higgins 1990, 1993; Higgins & Davies 1996; Higgins 1999; Higgins et al. 2001).

Hence new information is available to re-examine

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patterns of co-existence in Australia. A comprehensive analysis should ideally await completion of the last two volumes of the Handbook, so this paper will focus mainly on aspects familiar to this author, relating to birds that inhabit the eucalypt forests and woodlands of south-eastern Australia, and some more open dry-land habitats in the same region.

This paper takes a mainly descriptive approach, in the belief that ecological understanding needs to be based on a holistic combination of detailed studies at particular sites, and more broad-scale work to put those studies in their proper context. Several authors have recognised the need for a broad-scale approach, to cater for the dynamics of bird communities in space and time (Wiens 1981; Catterall et al. 1997; Clarke et al. 1999): this has led some authors to question the concept of communities as functional units (MacNally 1995). Previous analyses of ecological segregation have focused mainly on detailed studies of small groups of species (Ford 1985, 1989) but such studies tend to be conducted in areas where those species are common, leading to inevitable biases (Clarke 1997). This paper attempts to redress the balance and complement previous work by drawing more on broad-scale surveys and experience than on localised studies of selected species.

SEGREGATION MECHANISMS

Lack (1971) identified three main mechanisms by which closely related species may reduce competition through ecological isolation (range, habitat and feeding or food). Subsequent authors have sub-divided this list in various ways, and have debated the extent to which such mechanisms may arise through co-evolution, coincidence or other mechanisms (e.g. Tilman 1982). Essentially, the mechanisms translate to hierarchical degrees of co-existence and depend upon the degrees to which closely related species have differentiated ecologically. If species are segregated by range, with no overlap, it may be because they have evolved in isolation and never come into secondary contact. This is a common situation with pairs of species inhabiting mainland south-eastern Australia and either Tasmania (separated by Bass Strait, 200 km, since the last Ice Age 10,000 years ago) or south-west Western Australia (separated more recently by arid desert, ~1400 km). Such pairs of species do not need to develop mechanisms for ecological segregation, and evolutionary divergence will occur in response to a range of environmental factors and com-

petitive pressures from non-congeners. If species show some overlap in range, and remain as distinct species, it is instructive to examine segregating mechanisms in the zone of overlap. This may help understand the ecology of the species and the capacity of a habitat to support a diversity of species, regardless of whether the mechanisms have arisen through co-evolution or coincidence.

Often it emerges that these species are segregated by habitat, with substantial overlap in range at the broad scale but little or none at the fine scale. Some habitats are occupied by one species, others by the other, within a mosaic of habitats not easily distinguished in coarse maps of species range. More commonly, there may be some habitats occupied solely by one or other species, and others where the species can be found together. If a particular habitat is potentially suitable for more than one species, random chance, conflict, predation and physical aggression may be involved in determining the occupant of each territory. This form of co-existence is qualitatively different from that where clearly identifiable habitats are selected by each species: it involves random or competitive segregation of horizontal space within a habitat, rather than segregation by differential choice of habitat.

A higher level of co-existence occurs where species actually occupy the same area, at the scale of the individual home range or territory, as mapped on the ground. Maps are two-dimensional and forests have three spatial dimensions and a temporal dimension, so scope remains for such species to reduce competition by using different parts of the forest space or using them at different times. This may involve segregation by foraging height or substrate, or selection of different nesting or roosting sites. Such co-existence contributes to alpha-diversity of a habitat, and may be driven by the capacity of the habitat to support such diversity. Segregation by nesting or roosting sites may only be important where safe and effective nesting or roosting sites are in limited supply. Temporal segregation usually involves seasonal changes in abundance, though use of resources at different times of day is also possible, as are fluctuations in habitat quality between years. The ultimate level of co-existence occurs where species are able to use the same space at the same time in any dimension. Theory postulates that such co-existence is only likely to occur when species take different foods, or differ from each other in major morphological features such as size (Lack 1971; Tilman 1982).

This hierarchy of mechanisms will be used as a framework for examining ecological segregation in forest birds of south-eastern Australia, with its main focus on the eucalypt forests and woodlands of Victoria and adjacent mainland states (South Australia and New South Wales).

STUDY AREA AND METHODS

1) Rainfall and climate

Australia covers a wide range of latitudes, from the tropical north to the temperate south. It is essentially a dry continent, with high rainfall occurring only in the tropical north (during the monsoonal summer wet season), along the east coast and the adjacent Great Dividing Range, in Tasmania and in the south-western corner of Western Australia (Fig. 1). In temperate regions of southern Australia, more rain falls in winter and spring than at other times. Most birds in south-eastern Australia breed in late winter, spring and early summer. Patterns of bird migration and breeding are closely linked to seasonal conditions for plant growth (Nix 1976). Rainfall generally increases with altitude in the Great Dividing Range, and drops rapidly on the inland slopes of that range.

2) Vegetation

Sclerophyllous open eucalypt forests dominate the natural vegetation over most of temperate Australia (Groves 1981). In the mainland state of Victoria, vegetation has been classified and mapped by Ecological Vegetation Class (EVC), based on floristic analysis of understorey and overstorey. This classification has been useful for modelling animal distributions (e.g. large owls, Loyn et al. 2001) but it is too detailed for use at a general descriptive level. A national classification of "bioregions" has been developed by Thackway and Cresswell (1995) using biological and climatic data, and is in use as a planning tool in Victoria through the State Biodiversity Strategy (Government of Victoria 1997). A simpler summary of habitats according to their use by birds was provided by Loyn (1985a), and is further summarised below.

A wide range of eucalypt species grow in the varied coastal and foothill forests, usually as mixed stands containing several species. Stringybark species dominate the ridges and slopes (with some other eucalypts such as Silvertop *E. sieberi*), and peppermints and smooth-barked gums are prominent in the gullies. A high diversity of understorey species may include wattles *Acacia* spp., various shrubs and tangles

of Forest Wire-grass *Tetrarrhena juncea*. Tall shrubs and tree-ferns grow prolifically in wet gullies. Heaths develop on poor or sandy soils, with little or no tree cover and dense understorey dominated by grass-trees or proteaceous plants such as *Banksia* spp. Patches of closed warm temperate rainforest (dominated by non-eucalypts such as Lilly-pilly *Acmena smithii*) occur in damp sheltered gullies where wild-fires are rare. At higher elevations, stands of tall open forest are typically dominated by a smaller number of tree species or a single species such as Mountain Ash *E. regnans*, Alpine Ash *E. delegatensis* or Shining Gum *E. nitens*, with understoreys resembling those of foothill gullies. The trees include the tallest flowering plants in the world, with Mountain Ash growing to over 100 m on occasion. At higher elevations again, multi-stemmed trees of Snow Gum *E. pauciflora* form a low subalpine woodland.

On the drier inland slopes of the Great Dividing Range, mixed foothills forests give way to box-ironbark forests at low elevation, where annual rainfall is between 400–700 mm. Typically these open forests include a range of box eucalypt species along with Red Stringybark *E. macrorhyncha* and either Red Ironbark *E. sideroxylon*, Mugga Ironbark *E. mugga* or Yellow Gum *E. leucoxylon*. Understoreys are usually open, with many herbs, grasses, orchids and scattered shrubs. In the floodplain of the River Murray, forests are dominated by River Red Gum *E. camaldulensis* with open grassy understoreys, relying on seasonal floods for their productivity.

On sandy soils in more arid country, extensive mixed stands of short multi-stemmed mallee eucalypts grow in a band from north-western Victoria and



Fig. 1. Map of Australia, showing study region (circled).

south-western New South Wales through to Western Australia in the 300–400 mm annual rainfall zone. Stands of Black Box *E. largiflorens* often grow beside wetlands in these dry environments. Further inland, the vegetation is dominated by treeless chenopod shrublands or wattles such as Mulga *Acacia aneura*, with tall open woodland of River Red Gum growing along watercourses.

In this paper, all vegetation communities with trees are classed as forest or woodland. The discussion extends to include treeless vegetation (e.g. heathland, arid shrubland and cleared farmland), recognising the continuum that exists in the landscape as a result of rainfall gradients and human activities. Warm temperate rainforests occur northwards from eastern Victoria, and support a range of bird species that are not considered in this paper. Throughout south-eastern Australia, the low-lying forests in the 300–700 mm rainfall zone have been most subject to clearing, and forests are now heavily fragmented (Bennett et al. 1998). Forests at higher elevation in the Great Dividing Range are subject to a range of uses including logging, but largely remain as continuous forest. Many areas receive special protection as National or State Parks, or as Special Protection Zones or Special Management Zones within State Forest.

3) Bird fauna

Many Australian bird species are endemic to the Australasian region (Ford 1989; Schodde & Mason 1999). Molecular studies have shown that many major bird families have evolved in this region (which includes New Guinea and New Zealand), despite ecological and morphological similarities to families elsewhere in the world (Sibley & Alquist 1985). Waterbirds are not considered in this paper, although many of them depend heavily on seasonally inundated forests (or forests beside wetlands) for nesting and roosting sites.

4) Methods

This paper reviews some of the literature about ecology of forest birds, along with information based on personal experience. The aim is to document some interesting patterns of co-existence and competitive interactions among Australian forest and woodland birds, as a prelude to a possible more comprehensive analysis in future. The main focus is on pairs or groups of taxonomically similar species, and their means of co-existence or habitat segregation. Numerical analysis considered species pairs within genera

as currently defined by Christidis and Boles (1994) for non-passerines and Schodde and Mason (1999) for passerines.

In an attempt to quantify some of the ecological interactions for south-eastern Australian native land birds, all congeneric species were listed and grouped in pairs (1 pair for 2 species, 3 pairs for 3 species, up to 36 pairs for the maximum of 9 species). The analysis covered 48 genera, 148 species and 209 congeneric species pairs. The primary mechanism of ecological segregation was then identified for each species pair, along with any contributing mechanisms. Because differences in range or habitat can be identified for almost all species pairs, these were classified further to show the extent of overlap, on a scale from no overlap (separate ranges or completely distinct habitats within an overlapping range) to complete overlap where both species could always be found together. Segregation by range was recorded as the primary factor whenever there was no overlap in normal range. Segregation by foraging method, body size, type of food or stratum/substrate were scored whenever they appeared to be an important factor helping two species to share a habitat. However, just one mechanism was selected as the primary factor for each species. All factors would be expected to vary in detail between habitats as a secondary consequence of the different natures of each habitat (food availability, etc.) and such secondary differences were not scored. Comparisons were made between mean scores for species pairs with little or no overlap in range, and species pairs with substantial overlap in range.

RESULTS

1) Resource use by birds

Recher and Holmes (1985) compared the foraging methods used by Australian forest birds with those used by North American forest birds, and concluded that there were no substantial differences except where they related to special resources associated with Australian eucalypt forests. Two sets of special resources were identified. Firstly, many eucalypt forests produce copious flows of nectar and other carbohydrate exudates, both from the eucalypts themselves (via blossom and from insects and physical wounds) and from a wide range of understorey species (via flowers). These are an essential part of the diet of many honeyeaters, lorikeets and certain other bird species (e.g. Ford & Paton 1977, 1982;

Paton 1980). This resource is more dominant in eucalypt forests than in temperate forests elsewhere in the world (Recher & Holmes 1985). Some eucalypts such as box and ironbark species are particularly attractive to honeyeaters, as are blossoms from mistletoes, correas and Proteaceous plants. Heathland floras often include a wide range of plants that produce copious nectar flows at all times of year. Secondly, many eucalypts shed some of their bark on an annual basis, leaving smooth trunks or branches. The decorticating deciduous bark and hanging bark ribbons provide a unique feeding substrate not found in other forests. This deciduous bark habit contrasts with the evergreen nature of the foliage. The habit is most prevalent among eucalypts of the sub-genus *Symphymyrtus*, including species known as gum or ash (which typically have smooth-barked trunks) and some of those known as box which typically have smooth upper branches. The relative importance of different resources for birds in eucalypt forests can be assessed from the proportions of various guilds in the bird fauna (Loyn 1985a; Keast 1985).

2) Interspecific territoriality

A special feature of some Australian forests and woodlands, is that they become dominated by one or more bird species that aggressively exclude other birds, leading almost to sole occupancy of space by the aggressive species (Dow 1977). Usually the aggressive species are honeyeaters, although other species may be associated with them (e.g. Grey Butcherbird *Cracticus torquatus* and babblers *Pomatostomus* spp.). The situation always occurs in lowland or foothill forests or in open woodlands with a climate that supports populations of the species concerned throughout the year. It never occurs in mountain forests or in forests that are unable to support high resident populations of birds, such as those of low fertility on steep sites (Loyn 1985a,b; Emison et al. 1987). The species concerned have complex communal breeding systems (Dow 1978; Ford 1989; Clarke 1995, 1997), though such systems are not confined to this group of species.

The habit is best developed in the honeyeater genus *Manorina*, and applies to varying degrees with all four species in the genus (Higgins et al. 2001). The four species occupy different habitats on a mesic-xeric gradient from broad foothill gullies (Bell Miner *Manorina melanophrys*) through open woodland or small patches of fragmented forests (Noisy Miner *M. melanocephala*), open or fragmented stands

of mallee eucalypts (Yellow-throated Miner *M. flavigula*) to interiors of extensive mature mallee (Black-eared Miner *M. melanotis*). Their habitats sometimes join but rarely overlap, except with Yellow-throated and Black-eared Miners where a hybrid zone has developed after extensive clearing of mallee: Black-eared Miners are now listed as critically endangered. Miners take a wide range of food mainly from eucalypts, including arthropods, nectar and lerps (the sweet waxy inanimate covers produced by nymphs of psyllid insects). Patches of forest occupied by Bell Miners and Noisy Miners often show signs of defoliation by insects (Loyn et al. 1983; Loyn 1987a,b; Low 1994; Stone 1996). Bell Miners are the most aggressive of the four species and Black-eared Miners the least (Higgins et al. 2001). Only the latter allow other psyllid-eating birds to nest within their territories (Starks 1987; McLaughlin 1990; R. Clarke pers. comm.), though specialist psyllid eaters such as Striated Pardalotes *Pardalotus striatus* often make forays into territories occupied by other species before being expelled.

The effects of the miners' aggressive behaviour have been demonstrated in translocation experiments where miners were removed from their habitat and released elsewhere (Loyn et al. 1983; Loyn 1987a, b; Clarke & Schedvin 1997; Grey et al. 1997, 1998; Catterall et al. 1998 and in press). As Bell Miners were removed, other birds invaded and quickly reduced the populations of psyllid insects to negligible levels (Loyn et al. 1983; Loyn 1987b), before dropping to low levels commensurate with the reduced food supply. The invading birds included common forest honeyeaters, treecreepers and insectivores, and two species of parrot that also consumed psyllids at a higher rate than the Bell Miners had done. This demonstrated the power of common birds to control insects and the necessity for Bell Miners to live in a group and aggressively exclude other birds. It also led to the concept of Bell Miners "farming" the psyllids (Loyn 1987b), using a range of mechanisms to conserve the psyllid resource. Poiani (1993) presented evidence that Bell Miners are no more selective in taking lerps (sugary inanimate covers) and leaving psyllid nymphs than are other birds, suggesting that one of three mechanisms proposed to account for the efficacy of "farming" may not have been valid. However, this did not affect the main conclusions or the farming analogy itself (Loyn 1995). When Noisy Miners were removed from small forest patches, similar influxes of other birds occurred,

showing that the small forest patches are capable of supporting more diverse faunas in the absence of Noisy Miners (Grey et al. 1997, 1998; Catterall et al. 1998 and in press).

The eucalypt canopy recovered from defoliation over subsequent months after Bell Miner removal (Loyn et al. 1983): this may be one of the few published examples of a second-order vegetation response after manipulating predation pressure on insects. Responses after Noisy Miner removal appear to be more complex, and await further analysis. An unexpected result of this study was that Grey Butcherbirds abandoned the habitats from which Noisy Miners had been removed, suggesting a synergistic relationship between these species (Grey et al. 1998; M. Grey pers. comm.). Grey Butcherbirds have also been observed associating with colonies of Yellow-throated and Black-eared Miners in the mallee (pers. obs.; E. Moysey pers. comm.). The butcherbirds may benefit from high levels of resources such as large insects sequestered by the miners, and this relationship deserves further study.

In conclusion, interspecific territorial aggression appears to be a necessary mechanism for maintaining high levels of food supply necessary to support high year-round populations of the aggressive species (and perhaps their symbiotic partners such as Grey Butcherbirds). The system develops in habitats of high potential productivity and low seasonal climatic variability, and it usually involves cooperative breeding as well as interspecific aggression. From the evidence above, the degree of aggression needed appears to vary from high in mesic environments (where potential competitors are numerous) to low in xeric environments (where potential competitors are sparsely distributed). The distribution of Noisy Miners and Yellow-throated Miners suggests that exclusive territories may be easier to defend in fragmented environments than in continuous forest. This idea is supported by the distribution of Noisy Miners in natural forests such as Barmah State Forest, a 25,000 ha forest of River Red Gum on the Murray River. In and near that forest, Noisy Miners were confined to isolated patches of forest on grassy flood-plains, and to strips of roadside vegetation outside the forest (Chesterfield et al. 1984).

Although the habit is most pronounced among miners, many honeyeaters defend territories against a range of bird species (Collins & Briffa 1982; McFarland 1986; Ford 1989; Higgins et al. 2001) and may have a similar effect in reducing bird diversity and in-

creasing local resources available for themselves (Traill et al. 1996). White-plumed Honeyeaters *Lichenostomus penicillatus* have become common in fragmented rural forests and urban environments, partly excluding other honeyeaters (Loyn 1985a). Extensive box-ironbark forests are often occupied by two dominant species (Fuscous Honeyeater *L. fuscus* and the larger Yellow-tufted Honeyeater *L. melanops*), co-existing with each other but attacking other honeyeaters and insectivores (MacNally & McGoldrick 1997; Silveira et al. 1997). Their territories may overlap with those of White-plumed Honeyeaters on the edge of River Red Gum stands, with dynamic competition for space at the ecotone. Such competition may have excluded Fuscous and Yellow-tufted Honeyeaters from Barmah Forest, where stands of Grey Box *E. microcarpa* and Yellow Box *E. melliodora* form less than 5% of the forest area, and the niche is occupied solely by White-plumed Honeyeaters (Chesterfield et al. 1984).

The dynamics of aggressive communal birds such as these have profound implications for conservation. Local removal of Bell Miners has been found necessary to establish new habitat for the endangered Helmeted Honeyeater *Lichenostomus melanops cassidix* (Pearce et al. 1995; Menkhurst et al. 1999; Garnett & Crowley 2000). Similar measures with Noisy Miners may be needed to help conserve the endangered Regent Honeyeater *Xanthomyza phrygia*. However, longer term solutions must be found that involve habitat protection and restoration for these species, reducing the edge effects that have favoured aggressive miners. One of the miners (Black-eared Miner *M. melanotis*) is itself endangered, and needs protective measures in its interior mallee habitat (Starks 1987; McLaughlin 1990; Garnett & Crowley 2000; Higgins et al. 2001).

3) Segregation mechanisms

Of the 209 pairs of species examined (Appendix 1), 25 had distinct ranges with no overlap or close encounters and a further 25 had separate ranges that abutted each other with little or no overlap (Table 1). In all of these 50 cases the habitats were also distinctly different, with just two pairs (bristlebirds *Dasyornis* spp. and fieldwrens *Calamanthus* spp.) occupying structurally similar habitat in separate ranges (Appendix 1). Of the remaining 159 species pairs, 101 were segregated by habitat as the primary mechanism, with varying degrees of overlap. Across the whole sample of 209 pairs, substantial differences in

Table 1. Numbers of species pairs showing various primary mechanisms for ecological segregation in mainland south-eastern Australia, (a) among species pairs with little or no overlap in local range (scored as 0 or 1 in Appendix 1); (b) among species pairs with substantial overlap in local range (scored as 2+), and (c) among all species.

Mechanism	(a) Species pairs with little or no overlap in local range	(b) Species pairs with substantial overlap in local range	All species
Range (and habitat)	32	1	33
Habitat	17	102	119
Stratum or substrate	1	36	37
Size	0	11	11
Food or foraging technique	0	3	3
Nest site	0	2	2
Complex or unclear	0	3	3
None (i.e. appear ecologically very similar)	0	1	1
Total	50	159	209

foraging behaviour were identified for eight pairs, in size for 39 pairs, in food for 29 pairs and in stratum or foraging substrate for 96 pairs, in ways that may have contributed to ecological segregation though not necessarily as primary factors (Appendix 1). Nest sites usually reflected the preferred habitats and foraging strata, but seven pairs showed major differences in nest site that may have contributed to ecological segregation. Twenty-six pairs showed habitat differences that varied seasonally and the subject of bird movements and migration is discussed further below. In terms of primary mechanisms, it was judged that habitat was the main factor for 119 pairs, stratum or substrate for 37 pairs, range for 33 pairs, size for 11 pairs, food or foraging behaviour for three pairs, and nest site for two pairs (Table 1 and Appendix 1). One pair (of woodswallows *Artamus* spp.) showed no ecological differences and three pairs of honeyeaters showed complex differences that were hard to classify.

4) Patterns of species occurrence and co-existence in relation to habitat

Habitat differences were generally related to occurrence in broad forest types such as those described in the introduction. For example, three congeneric honeyeaters of similar size (Fuscous, White-plumed and Yellow-plumed) are the dominant species in box-ironbark forest, riverine or fragmented forests and mallee, respectively (Keast 1968; Ford & Paton 1976; Loyn 1985a; Emison et al. 1987; Higgins et al. 2001). They can be seen together where these habitats intermingle, or when drought or major flowering events

induce birds to move and use new food sources, but their normal breeding habitats show little overlap.

For many insectivores, density of trees and shrubs appears to be a key variable affecting occurrence of particular species, and this in turn is related to local climate and hydrology. For example, Yellow-rumped Thornbills *Acanthiza chrysorrhoa* feed mainly from the ground in open woodland or sparse chenopod shrublands, and also venture into treeless grassland or cleared farmland. Buff-rumped Thornbills *A. reguloides* feed from open ground but among trees (where they also take food from the bark). The similar Slender-billed Thornbill *A. iredalei* inhabits treeless heaths and chenopod shrublands, rarely mixing with Buff-rumped Thornbills even when the habitats are adjacent. Chestnut-rumped Thornbills *A. uropygialis* behave like Buff-rumped Thornbills but inhabit arid areas with a drier, more open type of woodland (e.g. Black Box) and associated chenopod shrublands. The contrast between Yellow-rumped and Buff-rumped Thornbills is reflected in the winter range of Flame Robin *Petroica phoenicea* and Scarlet Robin *P. boodang* (see below under bird movements), and the two species are often seen in loose association with the respective thornbills.

Several genera contain species that replace each other along xeric-mesic gradients, often with two occupying extreme habitats and a third generalist overlapping broadly with both. The granivorous bronzed-wing pigeons are an example. Flock Bronzedwings *Phaps histrionica* occur in sparsely treed arid and northern Australia (outside the region considered here for numerical analysis), overlapping in range

with Common Bronzewing *Phaps chalcoptera* but segregated by habitat, with the latter occurring among woodlands. Common Bronzewing has a wide continental range extending into open forests of the south-east, where they co-exist locally with Brush Bronzewing *Phaps elegans*. The latter is confined to southern Australia and occupies dense forest and coastal heath and dense stands of mallee. It is the sole species in some of these habitats with a dense tall shrub layer (e.g. tall wet forests of Mountain Ash *E. regnans*) (Loyn 1985a,b; Emison et al. 1987). However, in many forests and mallee both species can be found, selecting habitat according to the local density of shrub or eucalypt species. In areas of local food abundance (e.g. on recently logged coupes with abundant wattles *Acacia* spp.) both species can be seen feeding together along with a third ground-feeding pigeon, the Wonga Pigeon *Leucosarcia melanoleuca*. Breeding territories appear to be segregated by habitat at fine spatial scales, with little overlap. Similar patterns can be found among many insectivorous, nectarivorous and granivorous bird genera. Habitat selection appears to involve mutual choice rather than interspecific aggression in most cases other than honeyeaters (discussed above), with the robins *Petroica* spp. being a notable exception (see below under bird movements).

5) Patterns of species occurrence and co-existence in relation to stratum and substrate

Stratum or substrate was identified as a key primary or secondary (potential) segregating factor in more pairs of species with substantial range overlap (81/159=51%) than with little or no range overlap (15/50=30%) ($p < .01$) (Appendix 1). This suggests that it may be a common factor allowing similar congeners to occupy the same space. Stratum or substrate was identified as the primary segregating factor for 37 of the 209 species pairs (Table 1).

The trend was best developed in two species-rich families of birds (honeyeaters Meliphagidae and thornbills Acanthizidae), and may have contributed to the evolution and survival of so many species in these groups. Segregation in honeyeaters often involves differential use of resources such as nectar, honeydew, lerps and arthropods caught in aerial sallies or gleaned from leaves or bark, and these patterns have been well described (e.g. Keast 1968; Ford & Paton 1976, 1977, 1982; Collins & Briffa 1982; Paton 1980; Pyke 1983, 1985; Recher & Holmes 1985; Wykes 1985; McFarland 1986, 1988; Ford 1989;

Clarke & Clarke 1999; Higgins et al. 2001). For example, White-eared Honeyeaters *Lichenostomus leucotis* specialise at taking sap or honeydew from bark, and are common in environments such as Snow Gum woodlands and regrowth eucalypts where other honeyeaters are scarce (Wykes 1985; Loyn 1985a; Osborne & Green 1992). They co-exist with four or more congeners at intermediate levels of nectar resource, but are excluded from rich nectar sources by other honeyeaters. The number of species and diversity of foraging techniques allows for complex patterns of co-existence or exclusion at various spatial and temporal scales, and more detailed analysis of broad-scale patterns of abundance would be useful. Interspecific aggression also plays a major role in these species, with dominance hierarchies often excluding small species from the richest sources of nectar at a given time (Ford & Paton 1982; McFarland 1986; Ford 1989).

Thornbills are among the most common resident insectivores in many forests and woodlands where aggressive honeyeaters are unable to establish year-round exclusive territories (Loyn 1985a). Their foraging ecology has been studied by Recher et al. (1985), Recher and Holmes (1985) and Bell (1985). Three species co-exist in forests of the Great Dividing Range. Striated Thornbills *Acanthiza lineata* feed mainly in the eucalypt canopy and Brown Thornbills *A. pusilla* feed mainly among narrow-leaved shrubs, with Buff-rumped Thornbills feeding from bark and open ground in parts of the forest with sparse shrub layers. All three form mixed feeding flocks in winter, and their foraging niches expand when food is plentiful and contract when food is scarce (Bell 1985). The first two are so common that few areas of forest fail to support both species. In drier forest north or west of the Great Dividing Range a different set of species occupies similar niches, with Weebills *Smicrornis brevirostris* in the eucalypt canopy, Yellow Thornbills *A. nana* in narrow-leaved shrubs and either Buff-rumped, Yellow-rumped or Chestnut-rumped Thornbills feeding from the ground (depending on the stand density and aridity as discussed under Habitat). Some forests support both groups of thornbills, with segregation based firstly on fine-scale habitat and secondly on stratum (e.g. riverine and box-ironbark forests: Chesterfield et al. 1984; Traill et al. 1996; Silveira et al. 1997), but there is much overlap in some of these forests. Bill shapes have evolved to suit the respective lifestyles, with Striated Thornbills and Weebills having broad bills like pardalotes Pardalotidae, and

Brown Thornbills and Yellow Thornbills having fine bills for foraging among narrow-leaved shrubs.

6) Size, food and foraging technique

Size was identified as a partial segregating factor for 39 species pairs and the primary factor for ten of them. All of the latter were carnivores (hawks and owls) or nectarivores (lorikeets and honeyeaters). Some pairs of insectivores differed slightly in size but stratum or substrate was usually recognised as a more fundamental segregating mechanism in those cases. Many congeners take different foods (and use different foraging methods) as a result of their differences in size or preferences for particular substrates or strata. However, food preference was identified as a primary segregating mechanism for just two pairs. Little Wattlebirds *Anthochaera chrysoptera* show strong preferences for proteaceous flowers such as banksias *Banksia* spp., whereas Red Wattlebirds *A. carunculata* favour nectar from eucalypts (Paton & Ford 1977; McFarland 1986; Egan 1997; Higgins et al. 2001). They differ in size, often chase each other and sometimes feed together at abundant food sources, but the difference in food preference appears to be the most fundamental segregating mechanism. Glossy Black-Cockatoos *Calyptorhynchus lathami* are specialised for feeding on seeds of casuarinas *Alocasuarina* spp. whereas Yellow-tailed Black-Cockatoos *C. funereus* take a wide range of hard seeds and extract grubs from branches (Higgins 1999): again the difference in food preference appears to be fundamental. Foraging behaviour was identified as fundamental for just one pair: Grey Goshawks *Accipiter novaehollandiae* make more use of the "watch and pounce" hunting technique than do Brown Goshawks *A. fasciatus* (Olsen et al. 1990; Marchant & Higgins 1993). The two species also show substantial differences in diet, prey size and foraging habitat (Baker-Gabb 1984; Czechura 1985; Aumann 1988; Marchant & Higgins 1993) but the overlap in diet has been assessed as 50% (Olsen et al. 1990) and the differences may be driven by the difference in foraging behaviour.

7) Nest site

Each species has its own preferences for nest site, often related to preferred habitat or foraging stratum. Nest site was identified as the fundamental segregating mechanism for just two pairs. Spotted Pardalotes *Pardalotus punctatus* make their own tunnel nests in bare ground (Woinarski 1985), and use hollows in

trees only on an extremely local basis (S. Marchant pers. comm.). Striated Pardalotes *P. striatus* nest mainly in tree hollows, although they sometimes nest in loose groups in tunnels in sandy banks where such sites are available. The two species differ slightly in size and foraging methods, though both specialise at taking psyllid nymphs and lerps from eucalypt foliage (Woinarski 1985). Striated Pardalotes tend to favour smooth-barked eucalypts of the subgenus *Symphyomyrtus* (Loyn 1985a) and have a broader geographical range than Spotted Pardalotes. However, their ranges overlap extensively and they can often be found together, sometimes feeding simultaneously in the same trees (Woinarski 1985). Nest sites may limit both species, with Spotted Pardalotes needing patches of shrub-free open ground and Striated Pardalotes needing old trees with hollow spouts (Loyn 1998). These different needs may be of fundamental importance in allowing them to co-exist over broad areas of forest.

Nest sites also differed between the three swallows and martins, with Welcome Swallows *Hirundo neoxena* nesting on ledges (e.g. on open scars of old trees, and on houses and bridges), Fairy Martins *H. ariel* building bottle-shaped nests under overhangs or tunnelling into river-banks, and Tree Martins *H. nigricans* nesting mainly in hollow spouts of old trees. All species use buildings to various extents. The fundamental ecological segregation between Tree Martins and other species was identified as habitat, because Tree Martins nest mainly among trees and feed over forest and woodland (Blakers et al. 1984; Emison et al. 1987). However, it could be argued that this is a consequence of the preferred nest site. Welcome Swallows and Fairy Martins feed mainly in open country, where they are sometimes joined by non-breeding Tree Martins. The species differ somewhat in foraging method, with swallows swooping low over flat surfaces, and martins spending more time chasing insects high in the air. However, while breeding all three species are quite localised near suitable nesting sites. Hence it was concluded that the fundamental segregation between Welcome Swallows and Fairy Martins (and possibly between all three pairs) is based on nest site selection.

8) Complex patterns

Mechanisms of co-existence proved difficult to classify for three pairs of honeyeaters (Yellow-plumed Honeyeater *Lichenostomus ornatus* vs Purple-gaped Honeyeater *L. cratitius* and Grey-fronted

Honeyeater *L. plumulus*, and White-cheeked Honeyeater *Phylidonyris nigra* vs New Holland Honeyeater *Ph. novaehollandiae*), because of sparse information in the first cases and complexity in the third. Differences in habitat are likely to be the primary factor in the first cases, with Yellow-plumed Honeyeaters occupying dense stands of mallee eucalypts, Purple-gaped Honeyeaters reaching maximum density in mallee-heath or mallee-broombush and Grey-fronted Honeyeaters occupying a wide range of more arid habitats including sparse or young stands of mallee (Menkhorst & Davies 1983; Woinarski 1989; Higgins et al. 2001), but overlap is common, especially with Yellow-plumed and Purple-gaped Honeyeaters. White-cheeked Honeyeaters and New Holland Honeyeaters co-exist in heathlands of Western Australia and New South Wales (Blakers et al. 1984; Pyke 1985), but White-cheeked Honeyeaters are replaced by Crescent Honeyeaters *Phylidonyris pyrrhoptera* elsewhere in south-eastern Australia. New Holland Honeyeaters specialise at feeding from proteaceous flowers, and often dominate bird communities in heathlands where such flowers are abundant.

No evidence was found in this review for mechanisms such as predator-mediated co-existence (Sinclair 1995; Choquenot et al. 2001), though they may occur in some groups. Predation by native birds and introduced mammals may limit numbers of some Australian birds (Ford 1989), perhaps keeping them below levels where interspecific competition would arise. This could apply in particular to medium-sized ground-feeding birds such as bronzewings (discussed above).

One pair of species showed no ecological differences. White-browed Woodswallows *Artamus superciliosus* and Masked Woodswallows *A. personatus* often form mixed flocks and appear to be identical in their general ecology, travelling as highly mobile nomadic flocks and visiting rich food sources such as flowering eucalypts, concentrations of psyllids and lerps or swarms of plague locusts. They both inhabit a broad range across arid and semi-arid Australia, visiting less arid woodlands during times of drought. White-browed Woodswallows predominate in eastern Australia and Masked Woodswallows in western Australia but both species can be found to some extent throughout their range. No mechanism for ecological segregation is known.

9) Bird movements

In temperate parts of south-eastern Australia, many

bird species undertake regular migrations (Keast 1968; Nix 1976; Ford 1989; Clarke et al. 1999). Honeyeaters migrate by day and their visible migration has attracted much comment and detailed study (Hindwood 1956; Paton 1988; Munro & Wiltchko 1992; Munro et al. 1993; Munro & Munro 1998). Insectivorous birds also undertake highly predictable migrations, with a massive exodus of insectivores from wet forest in the Great Dividing Range for the winter and corresponding influxes in various parts of the country (Kikkawa & Pearse 1969; Recher et al. 1983; Loyn 1985a, b; Osborne & Green 1992; MacNally 1996; Catterall et al. 1997; Clarke et al. 1999). Some species are completely summer visitors to these forests (e.g. Satin Flycatcher *Myiagra cyanoleuca* and Rufous Fantail *Rhipidura rufifrons*) and others are completely summer visitors to wet forests (e.g. Grey Fantail *Rhipidura fuliginosa*) though some over-winter in dry forests. The commonest birds in these forests include resident insectivores (e.g. thornbills and treecreepers Climacteridae) and regular summer migrants such as Grey Fantail and Yellow-faced Honeyeater *Lichenostomus chrysops*. Yellow-faced Honeyeaters are largely insectivorous in summer, taking both insects and nectar from the eucalypt canopy, but switch to a more nectarivorous diet in their winter range. These regular patterns of migration provide opportunities for some species to share habitats by seasonal segregation. However, the reality is that movements track resources (Nix 1976) and the exodus of one species rarely provides opportunities for a related species to occupy vacated habitat. Just one example can be cited: Golden Whistlers *Pachycephala pectoralis* are winter visitors to lowland forests in the Murray-Darling Basin, and those same forests are occupied by Rufous Whistlers *P. rufiventris* in summer (Chesterfield et al. 1984; Loyn 1985a; Clarke et al. 1999).

A more common way in which migration allows species to share habitat, is that one species migrates and another does not: the two species share a habitat when resources are plentiful, and occupy separate habitats and ranges when resources are scarce. Golden Whistlers and Olive Whistlers *P. olivacea* share wet forest habitats in the breeding season, with further segregation by feeding stratum (Golden Whistlers foraging mainly among tall shrubs, and Olive Whistlers in the low shrub understorey). Golden Whistlers are common summer visitors to these forests whereas most Olive Whistlers remain over winter (Loyn 1985a, b). In some forest types

(e.g. foothill gullies containing Manna Gum *E. viminalis* and Narrow-leaf Peppermint *E. radiata*) Rufous Whistlers also occur as summer visitors, feeding in the eucalypt canopy. In those situations, all three species co-exist, segregated by foraging stratum. In the foothills, many Golden Whistlers may remain over winter, and their foraging extends into the eucalypt canopy when Rufous Whistlers have departed (Loyn 1985a). It is not known whether this behavioural change reflects the availability of food or the lack of competition from Rufous Whistlers.

The robins Petroicidae provide another example of this process. Scarlet Robins usually occupy dry forest habitats that can support resident pairs throughout the year, although they often need to expand their home range in winter (Robinson 1990, 1992). Flame Robins are regular migrants, totally vacating forest habitats in winter to congregate in farmland or open woodland. This habit allows them a greater choice of breeding habitat in the forests. Although they will compete aggressively with Scarlet Robins for territories in the foothills (Loyn 1980; Robinson 1992), the bulk of the population migrates to breed in wetter forest and at higher altitude (>800 m) where winter conditions would not support the resident species. Hence the migratory habit allows segregation by habitat, both in summer and winter, despite a large overlap where there is aggressive competition for space in the breeding season.

10) Interspecific associations

Many species form mixed-species flocks in winter and benefit in various ways such as early warning of predators and improved ability to find patchy resources (Bell 1985; Ford 1989). There may be more advantages in joining a mixed-species flock than a single-species flock, because ecological differences (as discussed above) will tend to reduce the total level of competition. There may also be direct benefits. Four examples can be cited from south-eastern Australian forests, based on well known but mainly anecdotal information. Firstly, Superb Lyrebirds *Menura novaehollandiae* forage by scratching vigorously at the forest floor, helping maintain understorey structure and regeneration (Ashton & Bassett 1997). In the process they displace more arthropods than they can catch or consume themselves. Lyrebirds are often followed by loose groups of other insectivores such as Eastern Yellow Robins *Eopsaltria australis*, White-browed Scrubwrens *Sericornis frontalis* and Pilotbirds *Pycnoptilus floccosus* that take advantage

of this revealed resource (Higgins et al. 2001). Secondly, many Grey Fantails migrate from foothill forests for the winter when flying insects are scarce, but those that remain spend substantial amounts of time following bark-foraging birds and catching winged insects displaced while those species forage behind loose bark. The main bark foragers concerned are White-throated Treecreepers *Cormobates leucophaea*, Red-browed Treecreepers *Climacteris erythrops*, Crested Shrike-tits *Falcunculus frontatus* and flocks of Varied Sittellas *Daphoenositta varia*. Both Grey Fantails and White-throated Treecreepers join mixed feeding flocks in winter (Bell 1985; Ford 1989). Thirdly, Willie Wagtails often concentrate their winter foraging round large mammals (kangaroos *Macropus* spp. or domestic stock), presumably benefiting from concentrations of insects near fresh warm dung. Fourthly, honeyeaters and other birds may congregate at fresh wounds in trees where marsupial possums or gliders (especially Yellow-bellied Gliders *Petaurus australis*) have made scars to extract exudates (Russell 1981; Loyn 1985b and unpublished; Chapman et al. 1999). These examples show how birds may benefit from the activities of unrelated birds and mammals in their environment.

DISCUSSION

The patterns of segregation revealed in this review resemble those described by Lack (1971) for continental avifaunas in various parts of the world. He identified habitat differences as much the commonest means of ecological isolation in continental passerines, and this is confirmed for the distinct group of birds inhabiting forests of south-eastern Australia. Differences of this sort allow multiple species to co-exist broadly in an area, but not to share habitats at the fine scale. Differences in foraging stratum or substrate were found to be important in allowing some species pairs to share the same habitat at the same time, increasing the diversity of those habitats. The species diversity of a given habitat is expected to be a function of its structural and floristic complexity, and those characteristics will set limits on the extent to which bird species can co-exist. Tilman (1982) presented a set of theoretical models for predicting outcomes of competitive exclusion and co-existence among organisms that may be useful in further interpretation of continental data on Australian birds.

The patterns identified differ in one respect from those described elsewhere, and that relates to the ag-

gressive honeyeater species that form interspecific territories (Dow 1977; Loyn et al. 1983; Loyn 1987a, b; Clarke 1995; Clarke & Schedvin 1997; Grey et al. 1997, 1998; Catterall et al. 1998 and in press). Ford (1989) discussed these species in relation to their communal breeding behaviour, and suggested that predator avoidance may have been a key driver for the evolution of communal breeding in these birds, many of which inhabit open and exposed woodland environments. A further reason is suggested by the experiments where Bell Miners were removed and other birds decimated their previously protected food supply: this showed that the level of resources needed to maintain the colony would not exist unless it was protected by an adequate number of birds within the group. Conversely, young birds would face great difficulties in establishing new territories without being part of a large enough group to maintain food supplies through territorial defence. A parallel situation has been reported for White-winged Choughs *Corcorax melanoleucos*, where young birds are encouraged to remain within the group (by kidnapping if necessary) in order to deter destructive attacks on the nest by other groups, in this case by conspecifics (Heinsohn 1987). Many factors contribute to evolution of communal breeding, but the ecological advantages (or necessities) of group living should be given due weight among them. Elsewhere in the world, various bird species appear to live as aggressive groups in temperate woodland habitats, and further work may show that communal defence of resources is an important factor in evolution of such systems.

This paper has focused mainly on ecological segregation between congeneric species, but the cases of interspecific aggression highlight the fact that competition occurs between all species, and can help determine the nature and health of the ecosystem. Woodland birds have declined in southern Australia (Robinson 1993; Barrett et al. 1994), and are vulnerable to competition from Noisy Miners in small grazed patches of forest (Loyn 1987a; Grey et al. 1997, 1998; Bennett 1999): active habitat management is needed to reverse such declines. A full analysis of competitive forces and the way they shape communities (Cody 1974; Kikkawa & Anderson 1984) must consider the full range of competing species. Species-based approaches will continue to be useful to conservation managers (e.g. Lambeck 1997; Loyn et al. 2001) but further understanding of ecological interactions will help progress to holistic ecosystem management.

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Appendix 1. Pairs of congeneric native bird species inhabiting forests, woodlands and shrublands of mainland south-eastern Australia (excluding species found mainly in warm temperate rainforest), showing the assessed primary mechanisms for ecological segregation along with other potentially important mechanisms, degree of overlap in total range (Australia) and local range (study region) and degree of habitat overlap in the study region.

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Phasianidae	<i>Coturnix pectoralis</i>	<i>C. ypsilophora</i>	h		2	2	1
	<i>Coturnix ypsilophora</i>	<i>C. chinensis</i>	h	sz	2	2	1
	<i>Coturnix pectoralis</i>	<i>C. chinensis</i>	h	sz	2	2	1
Accipitridae	<i>Accipiter fasciatus</i>	<i>A. novaehollandiae</i>	fg	fd	3	3	2
	<i>Accipiter novaehollandiae</i>	<i>A. cirrhocephalus</i>	sz	fg, fd	3	3	1
	<i>Accipiter fasciatus</i>	<i>A. cirrhocephalus</i>	sz	fg, fd	5	5	3
Columbidae	<i>Phaps chalcoptera</i>	<i>Ph. elegans</i>	h		3	3	3
Cacatuidae	<i>Calyptrorhynchus banksii</i>	<i>C. lathami</i>	r	sz, fd	2	0	2
	<i>Calyptrorhynchus banksii</i>	<i>C. funereus</i>	h		2	3	2
	<i>Calyptrorhynchus lathami</i>	<i>C. funereus</i>	fd		3	3	3
Psittacidae	<i>Trichoglossus haematodus</i>	<i>T. chlorolepidotus</i>	sz	fd	3	3	4
	<i>Glossopsitta concinna</i>	<i>G. pusilla</i>	sz		4	4	3
	<i>Glossopsitta pusilla</i>	<i>G. porphyrocephala</i>	h		2	2	1
	<i>Glossopsitta concinna</i>	<i>G. porphyrocephala</i>	h		2	2	1
	<i>Polytelis swainsonii</i>	<i>P. anthopeplus</i>	r		0	0	2
	<i>Platycercus elegans</i>	<i>P. eximius</i>	h	s	2	2	1
	<i>Neophema chrysostoma</i>	<i>N. pulchella</i>	h	m	1	1	0
	<i>Neophema chrysostoma</i>	<i>N. chrysogaster</i>	h	m	2	2	1#
	<i>Neophema chrysostoma</i>	<i>N. splendida</i>	h	m	2	3	0#
	<i>Neophema chrysostoma</i>	<i>N. petrophila</i>	h	n, m	1	0	0#
	<i>Neophema chrysostoma</i>	<i>N. elegans</i>	h		2	2	1#
	<i>Neophema elegans</i>	<i>N. chrysogaster</i>	h	m	1	1	0#
	<i>Neophema elegans</i>	<i>N. splendida</i>	h	m	2	1	1
	<i>Neophema elegans</i>	<i>N. pulchella</i>	r		0	0	0
	<i>Neophema elegans</i>	<i>N. petrophila</i>	h	n, m	2	1	1#
	<i>Neophema petrophila</i>	<i>N. pulchella</i>	r		0	0	0
	<i>Neophema petrophila</i>	<i>N. splendida</i>	r		0	0	0
	<i>Neophema petrophila</i>	<i>N. chrysogaster</i>	h	n, m	1	0	1#
	<i>Neophema chrysogaster</i>	<i>N. pulchella</i>	r		0	0	0
	<i>Neophema chrysogaster</i>	<i>N. splendida</i>	r		0	0	0
	<i>Neophema pulchella</i>	<i>N. splendida</i>	r		0	0	0
Cuculidae	<i>Cacomantis variolosus</i>	<i>C. flabelliformis</i>	s		2	4	3
	<i>Chrysococcyx osculans</i>	<i>Ch. basalis</i>	s		4	3	4
	<i>Chrysococcyx basalis</i>	<i>Ch. lucidus</i>	h		3	3	2
	<i>Chrysococcyx osculans</i>	<i>Ch. lucidus</i>	h		2	2	2
Strigidae	<i>Ninox strenua</i>	<i>N. connivens</i>	sz	fg, fd	3	2	1
	<i>Ninox connivens</i>	<i>N. novaeseelandiae</i>	sz	fd	3	3	4
	<i>Ninox strenua</i>	<i>N. novaeseelandiae</i>	sz	fd	3	3	4
Tytonidae	<i>Tyto tenebricosa</i>	<i>T. novaehollandiae</i>	h	fd, fg	3	3	1
	<i>Tyto novaehollandiae</i>	<i>T. alba</i>	sz	fd	3	3	2
	<i>Tyto tenebricosa</i>	<i>T. alba</i>	h	sz, fd, s	3	3	0
Caprimulgidae	<i>Eurostopodus mystacalis</i>	<i>E. argus</i>	h		1	1	1
Halcyonidae	<i>Todiramphus pyrrhopygia</i>	<i>T. sanctus</i>	h	sz	2	3	1
Climacteridae	<i>Climacteris affinis</i>	<i>C. erythrops</i>	r	fg, s	0	0	0
	<i>Climacteris erythrops</i>	<i>C. picumnus</i>	h	s	3	2	0
	<i>Climacteris affinis</i>	<i>C. picumnus</i>	s		2	3	2

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Maluridae	<i>Malurus cyaneus</i>	<i>M. splendens</i>	h		1	1	0
	<i>Malurus cyaneus</i>	<i>M. leucopterus</i>	h		1	2	0
	<i>Malurus cyaneus</i>	<i>M. lamberti</i>	h		2	2	2
	<i>Malurus splendens</i>	<i>M. leucopterus</i>	h	s	3	2	1
	<i>Malurus splendens</i>	<i>M. lamberti</i>	s		2	3	3
	<i>Malurus</i>	<i>M. leucopterus</i>	h	s	2	3	1
	<i>Stipiturus malachurus</i>	<i>S. mallee</i>	r		0	0	0
Pardalotidae	<i>Pardalotus punctatus</i>	<i>P. striatus</i>	n	sz, s	3	3	1
Acanthizidae	<i>Dasyornis brachypterus</i>	<i>D. broadbenti</i>	r		0	0	3
	<i>Sericornis frontalis</i>	<i>S. magnirostris</i>	s		3	3	4
	<i>Hylacola pyrrhopygia</i>	<i>H. cauta</i>	h		1	1	0
	<i>Calamanthus fuliginosus</i>	<i>C. campestris</i>	r		0	0	1
	<i>Gerygone mouki</i>	<i>G. fusca</i>	r		0	0	0
	<i>Gerygone fusca</i>	<i>G. olivacea</i>	h		2	2	3
	<i>Gerygone olivacea</i>	<i>G. mouki</i>	h		2	2	0
	<i>Acanthiza pusilla</i>	<i>A. chrysorrhoa</i>	h	s	3	4	0
	<i>Acanthiza pusilla</i>	<i>A. iredalei</i>	h		1	1	1
	<i>Acanthiza pusilla</i>	<i>A. nana</i>	h		3	3	2
	<i>Acanthiza pusilla</i>	<i>A. apicalis</i>	r		1	1	2
	<i>Acanthiza pusilla</i>	<i>A. uropygialis</i>	s		2	2	2
	<i>Acanthiza pusilla</i>	<i>A. reguloides</i>	s		3	4	3
	<i>Acanthiza pusilla</i>	<i>A. lineata</i>	s		4	5	4
	<i>Acanthiza apicalis</i>	<i>A. iredalei</i>	h	s	4	3	1
	<i>Acanthiza apicalis</i>	<i>A. lineata</i>	r	s	1	1	0
	<i>Acanthiza apicalis</i>	<i>A. reguloides</i>	s		1	2	2
	<i>Acanthiza apicalis</i>	<i>A. chrysorrhoa</i>	s		3	3	2
	<i>Acanthiza apicalis</i>	<i>A. uropygialis</i>	s		4	4	3
	<i>Acanthiza uropygialis</i>	<i>A. iredalei</i>	h	s	3	3	1
	<i>Acanthiza uropygialis</i>	<i>A. reguloides</i>	h		2	2	2
	<i>Acanthiza uropygialis</i>	<i>A. chrysorrhoa</i>	h		3	3	1
	<i>Acanthiza uropygialis</i>	<i>A. lineata</i>	s		1	1	1
	<i>Acanthiza uropygialis</i>	<i>A. nana</i>	s		2	3	3
	<i>Acanthiza reguloides</i>	<i>A. iredalei</i>	h	s	1	3	0
	<i>Acanthiza reguloides</i>	<i>A. chrysorrhoa</i>	h		3	3	1
	<i>Acanthiza reguloides</i>	<i>A. nana</i>	s		4	4	3
	<i>Acanthiza reguloides</i>	<i>A. lineata</i>	s		4	4	4
	<i>Acanthiza iredalei</i>	<i>A. nana</i>	h	s	1	3	1
	<i>Acanthiza iredalei</i>	<i>A. lineata</i>	h	s	1	1	0
	<i>Acanthiza iredalei</i>	<i>A. chrysorrhoa</i>	h		3	3	1
	<i>Acanthiza chrysorrhoa</i>	<i>A. lineata</i>	h	s	3	3	0
	<i>Acanthiza chrysorrhoa</i>	<i>A. nana</i>	s		2	4	2
	<i>Acanthiza nana</i>	<i>A. lineata</i>	s		3	3	3
Meliphagidae	<i>Anthochaera carunculata</i>	<i>A. chrysoptera</i>	fd	sz	3	3	2
	<i>Philemon corniculatus</i>	<i>Ph. citreogularis</i>	sz		3	2	3
	<i>Manorina melanophrys</i>	<i>M. melanocephala</i>	h	sz	3	2	0
	<i>Manorina melanophrys</i>	<i>M. flavigula</i>	r	sz	0	0	0
	<i>Manorina melanophrys</i>	<i>M. melanotis</i>	r	sz	0	0	0
	<i>Manorina melanocephala</i>	<i>M. flavigula</i>	h		2	2	0
	<i>Manorina melanocephala</i>	<i>M. melanotis</i>	h		3	2	0
	<i>Manorina flavigula</i>	<i>M. melanotis</i>	h		3	3	2

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
	<i>Lichenostomus chrysops</i>	<i>L. leucotis</i>	s	fd, m	2	3	3
	<i>Lichenostomus chrysops</i>	<i>L. melanops</i>	h	fd, s	3	3	1
	<i>Lichenostomus chrysops</i>	<i>L. virescens</i>	h	s	2	2	0
	<i>Lichenostomus chrysops</i>	<i>L. penicillatus</i>	h	s	2	2	1
	<i>Lichenostomus chrysops</i>	<i>L. cratitius</i>	r	s	1	1	0
	<i>Lichenostomus chrysops</i>	<i>L. ornatus</i>	r	s	1	1	0
	<i>Lichenostomus chrysops</i>	<i>L. plumulus</i>	r	s	1	0	0
	<i>Lichenostomus chrysops</i>	<i>L. fuscus</i>	h	s, m	5	3	1
	<i>Lichenostomus virescens</i>	<i>L. fuscus</i>	h	s	1	1	0
	<i>Lichenostomus virescens</i>	<i>L. leucotis</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. melanops</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. cratitius</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. penicillatus</i>	h	s	2	2	0
	<i>Lichenostomus virescens</i>	<i>L. ornatus</i>	h	s	3	3	1
	<i>Lichenostomus virescens</i>	<i>L. plumulus</i>	h	s	4	3	0
	<i>Lichenostomus leucotis</i>	<i>L. melanops</i>	h	fd, s	3	2	1
	<i>Lichenostomus leucotis</i>	<i>L. penicillatus</i>	s	sz, fd	2	2	1
	<i>Lichenostomus leucotis</i>	<i>L. ornatus</i>	s	sz, fd	3	3	2
	<i>Lichenostomus leucotis</i>	<i>L. fuscus</i>	s	sz, fd	3	2	1
	<i>Lichenostomus leucotis</i>	<i>L. plumulus</i>	s	sz, fd	2	3	1
	<i>Lichenostomus leucotis</i>	<i>L. cratitius</i>	s	sz, fd	3	3	1
	<i>Lichenostomus melanops</i>	<i>L. fuscus</i>	sz	s	4	4	4
	<i>Lichenostomus melanops</i>	<i>L. ornatus</i>	h	sz, s	1	1	0
	<i>Lichenostomus melanops</i>	<i>L. penicillatus</i>	h	sz, s	2	3	2
	<i>Lichenostomus melanops</i>	<i>L. plumulus</i>	r	sz, s	0	0	0
	<i>Lichenostomus melanops</i>	<i>L. cratitius</i>	r	sz, s	1	1	0
	<i>Lichenostomus cratitius</i>	<i>L. penicillatus</i>	h	s	2	3	0
	<i>Lichenostomus cratitius</i>	<i>L. fuscus</i>	r	s	1	1	0
	<i>Lichenostomus cratitius</i>	<i>L. plumulus</i>	h	s	2	3	3
	<i>Lichenostomus cratitius</i>	<i>L. ornatus</i>	?h	s	4	4	4
	<i>Lichenostomus ornatus</i>	<i>L. fuscus</i>	h		1	1	0
	<i>Lichenostomus ornatus</i>	<i>L. penicillatus</i>	h		2	2	0
	<i>Lichenostomus ornatus</i>	<i>L. plumulus</i>	?h	s	2	3	3
	<i>Lichenostomus plumulus</i>	<i>L. penicillatus</i>	h		2	2	0
	<i>Lichenostomus plumulus</i>	<i>L. fuscus</i>	r		1	0	0
	<i>Lichenostomus fuscus</i>	<i>L. penicillatus</i>	h	fd, s	2	3	1
	<i>Melithreptus gularis</i>	<i>M. brevirostris</i>	s	sz	2	3	3
	<i>Melithreptus brevirostris</i>	<i>M. lunatus</i>	s		2	3	3
	<i>Melithreptus lunatus</i>	<i>M. gularis</i>	s	sz, m	2	3	3
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. novaehollandiae</i>	h	fd, s	3	3	2
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. melanops</i>	h	fd, s	3	2	0
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. nigra</i>	r	fd, s	2	1	1
	<i>Phylidonyris pyrrhoptera</i>	<i>Ph. albifrons</i>	r		1	1	0
	<i>Phylidonyris novaehollandiae</i>	<i>Ph. melanops</i>	h	fd	3	3	1
	<i>Phylidonyris novaehollandiae</i>	<i>Ph. nigra</i>	c	s	2	2	3
	<i>Phylidonyris novaehollandiae</i>	<i>Ph. albifrons</i>	r		1	1	0
	<i>Phylidonyris nigra</i>	<i>Ph. melanops</i>	h	fd, s	2	2	1
	<i>Phylidonyris nigra</i>	<i>Ph. albifrons</i>	r	s	1	0	0
	<i>Phylidonyris albifrons</i>	<i>Ph. melanops</i>	h	fd, s	2	2	1
	<i>Epthianura tricolor</i>	<i>E. albifrons</i>	h		2	3	3

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Petroicidae	<i>Epthianura tricolor</i>	<i>E. aurifrons</i>	h		4	4	3
	<i>Epthianura aurifrons</i>	<i>E. albifrons</i>	h		2	3	4
	<i>Petroica boodang</i>	<i>P. phoenicea</i>	h	m	3	3	2\$
	<i>Petroica boodang</i>	<i>P. rosea</i>	h	s	2	3	1
	<i>Petroica boodang</i>	<i>P. goodenovii</i>	h		2	2	1
	<i>Petroica boodang</i>	<i>P. rodinogaster</i>	h		3	3	0
	<i>Petroica goodenovii</i>	<i>P. phoenicea</i>	h	m	2	2	0
	<i>Petroica goodenovii</i>	<i>P. rosea</i>	h	s	2	2	0
	<i>Petroica goodenovii</i>	<i>P. rodinogaster</i>	h		2	2	0
	<i>Petroica phoenicea</i>	<i>P. rodinogaster</i>	h	m	3	3	1
	<i>Petroica phoenicea</i>	<i>P. rosea</i>	h	s	2	3	1
	<i>Petroica rosea</i>	<i>P. rodinogaster</i>	s	m	2	4	3
Pomatostomidae	<i>Pomatostomus temporalis</i>	<i>P. superciliosus</i>	h		2	2	2
	<i>Pomatostomus superciliosus</i>	<i>P. ruficeps</i>	h		2	3	1
	<i>Pomatostomus temporalis</i>	<i>P. ruficeps</i>	h	s	2	2	1
Cinclosomatidae	<i>Psophodes olivaceus</i>	<i>P. nigrogularis</i>	r		0	0	0
	<i>Cinclosoma punctatum</i>	<i>C. castanotus</i>	r		0	0	0
Pachycephalidae	<i>Pachycephala olivacea</i>	<i>P. rufiventris</i>	s	m	2	3	2
	<i>Pachycephala olivacea</i>	<i>P. pectoralis</i>	s	m	3	3	3
	<i>Pachycephala olivacea</i>	<i>P. inornata</i>	h		0	0	0
	<i>Pachycephala olivacea</i>	<i>P. rufogularis</i>	r		0	0	0
	<i>Pachycephala rufogularis</i>	<i>P. inornata</i>	sz	fd	3	3	4
	<i>Pachycephala rufogularis</i>	<i>P. pectoralis</i>	s	sz	3	3	2
	<i>Pachycephala rufogularis</i>	<i>P. rufiventris</i>	s	sz	3	3	4
	<i>Pachycephala inornata</i>	<i>P. rufiventris</i>	s	m	3	3	4
	<i>Pachycephala inornata</i>	<i>P. pectoralis</i>	h		2	3	3
	<i>Pachycephala pectoralis</i>	<i>P. rufiventris</i>	s	m	2	3	2
Dicruridae	<i>Myiagra rubecula</i>	<i>M. cyanoleuca</i>	h		3	3	1
	<i>Myiagra cyanoleuca</i>	<i>M. inquieta</i>	s	sz, m	2	3	1
	<i>Myiagra rubecula</i>	<i>M. inquieta</i>	s	sz, m	2	2	2
	<i>Rhipidura rufifrons</i>	<i>M. fuliginosa</i>	s	m	3	3	4
	<i>Rhipidura fuliginosa</i>	<i>R. leucophrys</i>	h	s	3	3	1
	<i>Rhipidura rufifrons</i>	<i>R. leucophrys</i>	h	s	3	3	0
Campephagidae	<i>Coracina novaehollandiae</i>	<i>C. maxima</i>	h	s	3	3	3
	<i>Coracina novaehollandiae</i>	<i>C. papuensis</i>	h	sz	3	3	4
	<i>Coracina novaehollandiae</i>	<i>C. tenuirostris</i>	h	sz	3	3	3
	<i>Coracina papuensis</i>	<i>C. maxima</i>	h	s	2	1	1
	<i>Coracina papuensis</i>	<i>C. tenuirostris</i>	h		3	2	1
	<i>Coracina tenuirostris</i>	<i>C. maxima</i>	h	s	2	1	0
	<i>Artamus leucorhynchus</i>	<i>A. cyanopterus</i>	h		2	3	1
Artamidae	<i>Artamus leucorhynchus</i>	<i>A. personatus</i>	h		4	3	1
	<i>Artamus leucorhynchus</i>	<i>A. superciliosus</i>	h		4	3	1
	<i>Artamus leucorhynchus</i>	<i>A. cinereus</i>	h		4	4	0
	<i>Artamus personatus</i>	<i>A. cyanopterus</i>	h		3	4	2
	<i>Artamus personatus</i>	<i>A. cinereus</i>	h		5	3	1
	<i>Artamus personatus</i>	<i>A. superciliosus</i>	none!		5	5	5
	<i>Artamus superciliosus</i>	<i>A. cyanopterus</i>	h		3	4	2
	<i>Artamus superciliosus</i>	<i>A. cinereus</i>	h		5	3	1
	<i>Artamus cinereus</i>	<i>A. cyanopterus</i>	h	m	2	3	0
	<i>Cracticus torquatus</i>	<i>C. nigrogularis</i>	h	sz	2	2	2

Appendix 1. (Continued)

Family	Species 1	Species 2	Primary segregation mechanisms ¹	Other potentially important segregating mechanisms ²	Overlap in total range ³	Overlap in local range ³	Habitat overlap ⁴
Corvidae	<i>Strepera graculina</i>	<i>S. versicolor</i>	s	m	2	3	3
	<i>Corvus coronoides</i>	<i>C. tasmanicus</i>	h		2	2	1
	<i>Corvus coronoides</i>	<i>C. bennetti</i>	h		2	3	1
	<i>Corvus coronoides</i>	<i>C. mellori</i>	h		3	4	2
	<i>Corvus tasmanicus</i>	<i>C. mellori</i>	h		1	2	1
	<i>Corvus tasmanicus</i>	<i>C. bennetti</i>	r		0	0	0
	<i>Corvus mellori</i>	<i>C. bennetti</i>	r		2	2	1
Passeridae	<i>Taeniopygia guttata</i>	<i>T. bichenovii</i>	h		2	2	0
	<i>Stagonopleura guttata</i>	<i>S. bella</i>	h		2	2	0
Hirundinidae	<i>Hirundo neoxena</i>	<i>H. nigricans</i>	h	fg, s, m, n	2	4	2
	<i>Hirundo nigricans</i>	<i>H. ariel</i>	h	n	4	4	1
	<i>Hirundo ariel</i>	<i>H. neoxena</i>	n	fg, s, m	2	4	3
Sylviidae	<i>Cincloramphus mathewsi</i>	<i>C. cruralis</i>	h		4	4	0

¹ Ecological segregation mechanisms:

?=unsure; c=complex; fd=food; fg=foraging technique; h=habitat; m=migration; n=nest site; none!=none; r=range; s=stratum/substrate; sz=size. Range is given precedence to habitat as a primary mechanism, unless the two species occupy distinctly different habitats where their ranges join.

² Codes as above. Almost all species pairs show some differences in habitat and range, so these are not listed when considered only as secondary or potential mechanisms for ecological segregation. Degrees of overlap in range and habitat are described in the next three columns. The list of secondary mechanisms is not exhaustive.

³ Range overlap categories:

0=no contact; 1=ranges join, but little overlap; 2=substantial overlap; 3=range of one almost embraced by that of other, but latter covers much greater area; 4=ranges mostly overlapping, with range of one usually embraced by that of other; 5=ranges virtually identical.

⁴ Habitat overlap categories:

0=no overlap; 1=mainly separate habitats, but some overlap; 2=lots of separate habitat; substantial overlap too; 3=mainly overlapping but each species has separate habitats too; 4=one species has separate habitats but also completely overlaps habitat of the other species; 5=complete overlap. #=little or no overlap in breeding season, but may use similar habitats at other times. \$=less overlap in winter than in breeding season

Comparative foraging ecology of five species of ground-pouncing birds in western Australian woodlands with comments on species decline

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Abstract In this paper, we compare the foraging ecology of five Australian robins (*Petroica multicolor*, *P. goodenovi*, *Eopsaltria griseogularis*, *Microeca fascians*, and *Melanodryas cucullata*) in woodlands of Western Australia. Australian robins are insectivorous and obtain the greatest proportion of their prey by pouncing from a perch to the ground. Data were collected at three different sites in eucalypt (*Eucalyptus*) woodland and two sites in acacia (*Acacia*) woodland. The species differed in habitat, structure of the ground substrates where prey were taken, proportion of foraging manoeuvres used, height of foraging perches and prey-attack distances, though there were broad overlaps in all foraging dimensions. Within a site, species were more similar to each other in their foraging behaviour and selection of foraging substrates than they were to conspecific individuals occurring elsewhere. This indicates that potential foraging behaviours were very broad, and their expression is determined by the characteristics of the habitat and available prey. At all sites, robins took prey from ground substrates characterised by a mosaic of bare soil, low ground vegetation, and litter. The smallest species, *P. goodenovi*, used lower perches than the other robins and probably searched for small prey which it located at short distances. *P. goodenovi* had the widest distribution and was the most abundant of the species studied. The implications of these findings for the conservation of ground-foraging birds in Australia are discussed.

Key words Foraging ecology, Ground-pouncing birds, Petroicidae, Threatened species conservation, Woodlands

Ground-foraging birds are common in Australian woodlands (Recher et al. 1985; Ford et al. 1986; Recher & Davis 1997, 1998). Among them are species which search for prey from a perch and pounce on ground-dwelling invertebrates and small vertebrates. This pouncing guild is comprised of such different birds as kingfishers (Alcedinidae), cuckoos (Cuculidae), Australian robins (Petroicidae), and butcherbirds (Artamidae), all of which are important components of bird communities in Australian woodlands and forests (Recher et al. 1985; Holmes and Recher 1986).

In this paper, we compare the foraging ecology of

five Australian robins (Scarlet Robin *Petroica multicolor*, Red-capped Robin *P. goodenovi*, Western Yellow Robin *Eopsaltria griseogularis*, Jacky Winter *Microeca fascians*, and Hooded Robin *Melanodryas cucullata*) in eucalypt (*Eucalyptus*) and acacia (*Acacia*) woodlands of Western Australia. All are insectivorous and only rarely take small vertebrates and seeds (Barker & Vestjens 1990). Our objective is to describe the foraging behaviour of each species and the structure of the ground habitats from which they obtain prey. Previous studies of ground-foraging birds in Australia have considered the ground as a single substrate (e.g., Recher & Davis 1997, 1998), but the ground surface is a mosaic of vegetation, litter, bare ground and coarse woody debris. There is therefore the potential for ground-foraging birds to

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partition different parts of this mosaic and minimize competition for food resources on what is otherwise a single, horizontal plane. Thus, in considering the partitioning of foraging resources among ground-pouncing birds, our emphasis is on micro-habitat selection of ground substrates. Because ground-foraging birds are among the most threatened on the Australian continent (Recher 1999; Garnett & Crowley 2000), we conclude with comments on the reasons for their decline.

METHODS

1) Study Sites

Data were collected in Western Australia from June to October 1997 in Wandoo *Eucalyptus wandoo* and Powderbark Wandoo *E. accedens* woodlands in Dryandra State Forest (centred on 32°45'S, 116°55'E; 400 m asl) near the town of Narrogin; in mallee and Wheatbelt Wandoo/York Gum (*E. capillosa*/*E. loxophleba*) woodlands in Durrakoppin Nature Reserve near Kellerberrin (31°07'S, 117°13'E; 350 m asl); and in Salmon Gum/Gimlet/Morrel (*E. salmonophloia*/*E. salubris*/*E. longicornis*) woodlands at Yellowdine (31°22'S, 119°09'E; 400–450 m asl) east of Southern Cross. During July and August 1999, we collected data on ground-pouncers in woodlands dominated by *Acacia* spp. near Gascoyne Junction (25°03'S, 115°12'E; 150 m asl) and Mt Magnet (28°04'S, 117°20'E; 375–400 m asl). Sites were selected where birds, including ground-pouncers, were abundant.

None of the eucalypt woodlands in which we worked was grazed by domestic stock, nor had any been recently burnt. Winter rainfall in 1997 was average with good herbaceous and shrub growth on all sites. In contrast, the *Acacia* woodlands at Gascoyne Junction and Mt Magnet were grazed heavily by sheep, goats and cattle and had significant soil degradation and loss. This was particularly so for the Mt Magnet area. There was no evidence of recent fires. Both sites had had two seasons of above average rainfall. Where it survived grazing by domestic animals, ground vegetation in the acacia woodlands had an abundance of green foliage, flowers and seed.

2) Birds

Although we sought out as many different pairs and individuals as possible, we inevitably recorded data on the same individuals on more than one occasion. Appendix 1 presents the number of observed foraging manoeuvres for each species at each site and

the estimated minimum number of pairs for which data were obtained. In 1997, only Red-capped (RCR), Scarlet (SR), and Western Yellow Robins (WYR), and Jacky Winter (JW) were present at Dryandra. For comparison of foraging behaviour, we therefore include observations of Hooded Robins (HR) at Dryandra made in 1995 (Recher & Davis 1998; unpubl.), but these were not used in analyses as conditions between the years differed and the ground substrates around perches were not recorded in 1995. Jacky Winter and Red-capped Robin occurred at Durrakoppin and Yellowdine, but only Red-capped Robins were found at Gascoyne Junction. At Mt Magnet, Hooded and Red-capped Robins were present, but despite extensive searching only two pairs of Hooded Robins were found (Appendix 1).

All data were collected during the breeding season (August–October) and individuals were nesting or feeding fledglings at the time of observation. None of the data is from birds in their year of hatching. Morphological data were obtained from Baker et al. (1997; see Appendix 2).

3) Foraging Data

For each individual encountered, we recorded up to five consecutive foraging manoeuvres (prey-attacks) following the procedures and terminology of Recher et al. (1985). Following Recher and Gebski (1990), the first manoeuvre observed was not recorded; records commenced with the second manoeuvre observed. For each observation, we recorded species, sex (if known), foraging manoeuvre, perch height, height and substrate of prey, and horizontal distance along the ground to prey from perch (distance of attack). For some observations, perch height and/or the distance of attack was not recorded, usually because they were not seen clearly. For this reason, some sample sizes differ between tables.

4) Foraging Habitat

The habitats in which robins occurred were noted, but we did not quantify habitat attributes other than the ground substrates where prey were taken. We measured ground substrates used for foraging in the following way. As we followed foraging robins, perches from which a bird pounced to the ground were flagged with numbered, coloured tape so that they could be located later.

Within a three metre radius of each perch, we estimated percent cover of logs, coarse woody debris (e.g., branches, fallen dead shrubs), litter (e.g., dead

leaves, shed bark), bare ground, ground vegetation (grass, ferns and herbs), trees, and shrubs, and the number of trees and shrubs. The three metre radius was selected following earlier work (Recher and Davis unpubl.) which had shown that the average distance from perch to prey for ground-pouncers was within three metres for all species. In the work reported here, we assumed that the entire three metre circle around a perch was searched equally for prey.

As the measurements made were of superimposed layers of vegetation, debris and litter, total cover can exceed one hundred percent. Birds often moved short distances (<3 m) between perches, or pounced repeatedly from the same perch. We only recorded habitat data for successive pounces if the perches used were at least 6 m apart (i.e., no overlap of the 3 m radius circles around perches). Substrate measurements are therefore fewer than the recorded number of pounces.

5) Analysis

We used all observations in the comparison of differences in foraging behaviour and set the accepted level of significance at $P < 0.01$ to compensate for the lack of independence of some data (see Recher and Gebiski 1989 for a justification of these procedures). Some rare behaviours (<1% of observations) were grouped with more common behaviours: hovering manoeuvres were combined with hawk and probe was combined with glean. Some infrequent behaviours (1–5% of observations) (e.g., pounce bark, glean foliage) were grouped together as others and not included in analyses because of the large number of zero (nil) observations among species and sites.

As we could not always confirm the sex of individuals or for species which are not sexually colour dimorphic, data for males, females and individuals of unknown sex were combined.

All statistical tests were carried out using 'Statistica for Windows' (Statsoft Inc. 1999). Loglinear analyses were used to compare foraging manoeuvres between plots and species. Differences between species and site in the use of substrates were not tested as inspection of the data showed a high correlation between foraging manoeuvre and substrate. Correlations were also calculated between perch height and distance of attack. Correlations were calculated separately for species and sites because of differences in the structure, height and floristic composition of the vegetation between sites.

Only the Red-capped Robin was present at all

sites, so the 3-way table showing foraging behaviour for all species at all sites was incomplete. However, it was possible to construct a complete 3-way table (species \times site \times foraging manoeuvre) for Red-capped Robin and Jacky Winter at Dryandra, Durrakoppin and Yellowdine. For Hooded and Red-capped Robins at Mt Magnet, and for Jacky Winter, Red-capped, Scarlet and Western Yellow Robins at Dryandra, 2-way tables (species \times manoeuvre) were constructed.

MANOVA was used to test for differences between species and sites in two foraging attributes (perch height and attack distance) and four habitat attributes (% shrub cover, % bare ground, % ground vegetation and % litter, including coarse woody debris and logs). Prey height was excluded because of the high frequency of 0 height (i.e., the prey were on the ground).

Not every species was present at each site, so we first tested for differences between each species at each site. Jacky Winter and Red-capped Robin occurred at more than one site, so subsequent analyses tested for differences across sites for each of these. Dependent variables in MANOVA were screened for conformity to assumptions and transformed if necessary; perch height and attack distance were log-transformed to meet MANOVA assumptions and all percent data were arcsine transformed (Tabachnik & Fidell 1996). Initial multivariate tests used a significance level of $P < 0.01$, but univariate tests after an initial multivariate test was significant used $P < 0.05$.

The habitat attributes (% shrub cover, % bare ground, % ground plants and % litter) of each individual attack in which the bird pounced on ground-dwelling prey were also assessed using MANOVA (see Table 5 which includes omitted variables for completeness). The pattern of analyses follows that for foraging attributes.

The means of the habitat variables and the means of the foraging variables for each species at each location were standardised before being subjected to cluster analysis based on complete linkage and Euclidean distances. The distance matrix from the clustering exercise was then used in multi-dimensional scaling (MDS) to determine if distinct groups of species or locations could be classified on the basis of habitat and foraging variables. In MDS, the axes do not have a numerical value and are expressed simply as dimensions without units (i.e., a visual picture) and are not proportional to the variances described.

Table 1. Foraging behaviour of ground-pouncing robins at five sites in *Eucalyptus* and *Acacia* woodlands in Western Australia: Red-capped Robin (RCR); Scarlet Robin (SR); Jacky Winter (JW); Western Yellow Robin (WYR); Hooded Robin (HR). Numbers are percent of combined manoeuvre/substrate prey attacks. Sample size is given in parenthesis. See Appendix 1 for the number of pairs for which data were recorded.

Manoeuvre	Foraging behaviour						Others ²
	Pounce Ground	Glean Ground.....Bark	Hawk Air	Snatch Foliage.....Bark			
A. <i>EUCALYPTUS</i> Woodlands							
Dryandra							
RCR (158)	74	6	1	6	4	6	3
SR (189)	80	1	3	5	7	3	1
JW (206)	64	0	0	15	10	10	1
WYR (198)	93	0	0	2	2	1	2
HR (41) ¹	80	0	15	0	5	0	0
Durrakoppin							
RCR (75)	83	1	1	7	5	1	2
JW (86)	52	0	7	25	1	15	0
Yellowdine							
RCR (55)	38	5	11	35	0	2	9
JW (73)	29	0	1	55	4	11	0
B. <i>ACACIA</i> Woodlands							
Gascoyne							
RCR (69)	59	0	6	20	10	1	4
Mt Magnet							
RCR (92)	79	3	9	4	1	1	3
HR (66)	89	0	0	2	3	0	6

¹ 1995 data adapted from Recher and Davis (1998); ² includes glean foliage, pounce bark

RESULTS

1) Foraging manoeuvres and substrates

Table 1 combines the substrate of the prey with the foraging manoeuvre of the bird for the most common foraging behaviours. Except at Yellowdine, ground-pouncing was the most frequent foraging behaviour recorded and ground was the most common foraging substrate (Table 1). Hawking insects from the air and snatching prey from foliage and bark were the next most common behaviours and were the most frequent behaviours at Yellowdine. Red-capped Robins often gleaned prey, usually from the ground or bark, as did Hooded Robins at Dryandra in 1995 (Table 1). Red-capped robins sometimes hopped along the ground and gleaned prey from the soil surface, litter and low (<2 cm high) vegetation. At Yellowdine, 5% of prey taken by Red-capped Robins were gleaned from the foliage of ground vegetation. Birds hopping on the ground also snatched prey from low vegetation or hawked it from the air.

Loglinear analysis of the 3-way table (species ×

site × foraging manoeuvre) for Red-capped Robins and Jacky Winters fitted a model involving significant 2-way interactions between behaviour and species ($\chi^2_3=49.29$, $P<0.01$) and between behaviour and site ($\chi^2_6=201.16$, $P<0.01$). A higher proportion of Jacky Winter foraging behaviour was spent in hawking insects from the air and less pouncing to the ground than for Red-capped Robin. At Yellowdine, both hawked more frequently and pounced less often than elsewhere (Table 1).

At Dryandra, there was a significant difference in foraging manoeuvres between bird species ($\chi^2_4=18.05$, $P<0.01$). Western Yellow Robins differed from other robins by taking almost all prey by pouncing (93%) and rarely snatching, hawking or gleaning (Table 1). Jacky Winters hawked and snatched prey more frequently than Scarlet and Red-capped Robins. In a 2-way comparison, there was no difference between Red-capped and Scarlet Robins ($\chi^2_3=3.52$, $P>0.25$).

At Mt Magnet, there was no significant difference in foraging manoeuvres between species ($\chi^2_6=3.94$,

Table 2. Mean perch height and attack distance in meters for five species of ground-pouncing robins at five sites in Western Australian woodlands: Red-capped Robin (RCR), Scarlet Robin (SR), Jacky Winter (JW) and Western Yellow Robin (WYR). Standard deviation shown in parenthesis. Hooded Robin (HR) data for Dryandra were obtained in 1995 (Recher and Davis unpubl.). Heights and distances are for ground-pouncing foraging manoeuvres only. Perch height and/or attack distance were not always recorded, while dashes indicate the species was absent from that site.

Species	Site				
	Dryandra	Durrakoppin	Yellowdine	Gascoyne Junction	Mt Magnet
RCR					
No. observations	117	62	22	36	34
Perch height	1.2 (1.0)	1.3 (0.8)	1.5 (1.3)	1.3 (1.1)	0.8 (0.5)
Attack distance	1.9 (1.7)	1.5 (1.3)	3.6 (3.0)	1.8 (1.9)	1.5 (1.3)
SR					
No. observations	53	—	—	—	—
Perch height	1.5 (1.0)	—	—	—	—
Attack distance	2.6 (2.1)	—	—	—	—
JW					
No. observations	129	45	22	—	—
Perch height	1.5 (1.0)	2.1 (1.1)	1.9 (1.6)	—	—
Attack distance	2.3 (1.8)	2.8 (1.8)	3.6 (3.7)	—	—
WYR					
No. observations	83	—	—	—	—
Perch height	1.5 (0.9)	—	—	—	—
Attack distance	2.5 (2.2)	—	—	—	—
HR					
No. observations	15	—	—	—	52
Perch height	2.1 (1.1)	—	—	—	1.1 (0.8)
Attack distance	3.7 (1.7)	—	—	—	2.3 (2.5)

$p=0.03$). However, gleaning comprised 12% of foraging manoeuvres for the Red-capped Robin, but the Hooded Robin did not glean (Table 1).

Red-capped Robins used similar proportions of foraging manoeuvres and substrates at Dryandra and Durrakoppin ($\chi^2_3=1.68$, $P>0.5$), but they pounced less, and hawked and gleaned more at Yellowdine than at Dryandra and Durrakoppin ($\chi^2_3=46.37$, $P<0.01$) (Table 1). Red-capped Robins at Gascoyne Junction pounced less and hawked and snatched more than at Mt Magnet ($\chi^2_1=7.49$, $P<0.01$) (pounce vs all other behaviours combined).

There was no difference in the behaviour of Jacky Winters between Dryandra and Durrakoppin ($\chi^2_1=3.37$, $P>0.1$) (pounce vs all other behaviours combined), but birds at Yellowdine pounced less and hawked more than at the other sites ($\chi^2_4=42.47$, $P<0.01$) (glean and other' categories deleted) (Table 1).

The behaviour of Hooded Robins at Dryandra in 1995 was similar to that of Hooded Robins at Mt

Magnet in 1999, but the Dryandra birds took 15% of their prey by gleaning bark. At Mt Magnet, Hooded Robins took 6% of prey by gleaning foliage (Table 1).

2) Perch height and distance of attack

Although robins occasionally took prey at distances exceeding six metres, most prey were taken within three metres of the perch from which it was sighted (Table 2). Except for Red-capped Robin at Yellowdine, 10 of the 11 species/site comparisons of perch height and attack distance were significantly correlated: the higher the perch, the greater the distance at which prey were attacked (Table 3). For six of the seven comparisons possible, robins used higher perches when hawking than for ground pouncing (Table 4). However, sample sizes were small and the differences were not always significant (Table 4).

Initial MANOVA at Dryandra found that species differed significantly (Wilks lambda_(21,1404)=0.97, $P<0.001$). Univariate tests revealed that these differ-

Table 3. Correlation coefficients between perch height and distance of attack for Red-capped Robin (RCR), Scarlet Robin (SR), Jacky Winter (JW), Western Yellow Robin (WYR), and Hooded Robin (HR) at five sites in eucalypt and acacia woodlands in Western Australia during 1997 and 1999. Data includes all available foraging behaviours including ground-pouncing and hawking (sally). Sample size is in parenthesis. (** $P < 0.001$, * $P < 0.01$, NS – not significant, $P > 0.01$). Dashes indicate species was absent from that site in 1997.

Species	Site				
	Dryandra	Durrakoppin	Yellowdine	Gascoyne Junction	Mt Magnet
RCR	0.39**(130)	0.62**(62)	0.32 (NS)(41)	0.71**(41)	0.46**(56)
SR	0.30**(165)	–	–	–	–
JW	0.31**(163)	0.66**(45)	0.82**(21)	–	–
WYR	0.45**(188)	–	–	–	–
HR	–	–	–	–	0.70**(53)

Table 4. Mean perch heights of ground pouncing robins compared to the perch heights of robins hawking and snatching. Species and sites without perch height data for hawking and snatching robins have been deleted. All P-values are significant using $P = 0.0014$, after Bonferroni correction from an initial P of 0.01.

Site	Species	GP Ht	Hawk Ht	t	P
Dryandra	RCR	1.15 (106)	1.08 (4)	$t_{(88)} = 0.13$	0.89
	SR	1.63 (137)	2.52 (4)	$t_{(139)} = 1.62$	0.11
	JW	1.51 (134)	3.26 (34)	$t_{(166)} = 4.92$	<0.0001
Durrakoppin	JW	2.10 (45)	3.18 (20)	$t_{(63)} = 3.32$	0.001
Yellowdine	RCR	1.47 (290)	5.13 (18)	$t_{(35)} = 7.34$	<0.0001
	JW	1.90 (22)	4.82 (41)	$t_{(61)} = 3.04$	0.003
Gascoyne	RCR	1.26 (36)	2.61 (7)	$t_{(41)} = 3.19$	<0.003

ences were related to differences in perch height ($F_{3,642} = 4.53$, $P < 0.01$) and attack distance ($F_{3,642} = 3.23$, $P = 0.02$). Red-capped Robins used lower perches and attacked prey closer to the perch than co-occurring robins (Table 2). Scarlet Robins, Jacky Winters and Western Yellow Robins used the same height perches and attacked prey at similar distances (Table 2). At 2.1 m, the perch height of Hooded Robins at Dryandra in 1995 was greater than for other robins at Dryandra in 1997 (Table 2).

Initial MANOVA at Durrakoppin found strong differences between the species (Wilks lambda $_{2,104} = 0.82$, $P < 0.001$), while univariate tests revealed that these were caused by variation in perch height ($F_{1,105} = 15.19$, $P < 0.001$) and distance of attack ($F_{1,105} = 21.24$, $P < 0.001$). Red-capped Robins perched lower and attacked prey at closer distances than Jacky Winters (Table 2).

No significant interspecific differences in foraging attributes occurred at either Yellowdine or Mt Magnet at the 0.01 level (Wilks lambda $_{2,59} = 0.90$, $P = 0.045$;

Wilks lambda $_{2,119} = 0.98$, $P = 0.39$, respectively).

Initial MANOVA found significant differences between locations for Red-capped Robin (Wilks lambda $_{8,686} = 0.81$, $P < 0.001$), which univariate tests attributed to perch height ($F_{4,325} = 15.48$, $P < 0.001$) and distance of attack ($F_{4,325} = 3.77$, $P = 0.005$). Perch height at Yellowdine was markedly higher than other sites (Table 2). Attack distances varied considerably, with the greatest values at Yellowdine (Table 2). There were significant differences in the foraging attributes of Jacky Winter between Durrakoppin, Dryandra and Yellowdine (Wilks lambda $_{4,450} = 0.94$, $P = 0.005$), which univariate tests attributed to differences in perch heights ($F_{2,226} = 7.26$, $P < 0.001$). Perch heights at Durrakoppin and Yellowdine were similar, but higher than those at Dryandra (Table 2).

3) Characteristics of foraging habitat

Initial MANOVA at Dryandra found that species differed significantly (Wilks lambda $_{12,1307} = 8.60$, $P < 0.001$). Univariate tests revealed that these differ-

Table 5. Habitat characteristics of ground substrates of Western Australia eucalypt and acacia woodlands on which Red-capped Robin (RCR), Scarlet Robin (SR), Jacky Winter (JW), Western Yellow Robin (WYR), and Hooded Robin (HR) hunted for prey. Sample size (N) is shown in parentheses. Measurements are based on a three metre radius around the perch from which the bird attacked prey. Values are means \pm standard deviation.

Location	% Cover						
	Trees	Shrubs	Ground vegetation	Logs	Coarse woody debris	Litter	Bare ground
Dryandra							
RCR (122)	13 \pm 17	9 \pm 12	24 \pm 25	1 \pm 3	5 \pm 7	42 \pm 27	30 \pm 29
SR (140)	14 \pm 12	8 \pm 12	31 \pm 26	3 \pm 4	5 \pm 6	46 \pm 26	18 \pm 19
JW (111)	16 \pm 10	4 \pm 7	22 \pm 23	3 \pm 5	4 \pm 3	44 \pm 25	29 \pm 26
WYR (156)	17 \pm 16	10 \pm 14	21 \pm 22	4 \pm 5	3 \pm 5	57 \pm 28	17 \pm 19
Durrakoppin							
RCR (63)	15–20 ¹	8 \pm 13	47 \pm 24	3 \pm 6	no data ²	34 \pm 24	16 \pm 16
JW (48)	15–20 ¹	10 \pm 13	30 \pm 19	4 \pm 6	no data ²	41 \pm 21	25 \pm 23
Yellowdine							
RCR (20)	12 \pm 14	17 \pm 16	1 \pm 2	2 \pm 3	8 \pm 6	35 \pm 29	44 \pm 22
JW (27)	12 \pm 13	6 \pm 10	2 \pm 2	4 \pm 4	5 \pm 5	48 \pm 26	43 \pm 25
Gascoyne junction							
RCR (21)	10 \pm 20	15 \pm 13	13 \pm 11	1 \pm 2	6 \pm 5	21 \pm 19	59 \pm 21
Mt Magnet							
RCR (55)	15 \pm 20	14 \pm 14	14 \pm 16	0	2 \pm 3	23 \pm 16	59 \pm 19
HR (43)	21 \pm 22	5 \pm 6	16 \pm 12	0	3 \pm 4	18 \pm 16	62 \pm 19

¹ Range of projected canopy cover for study site as measured by HFR in 1986.

² At this site, coarse woody debris was included with litter as a single measure.

ences were caused by differences in % shrub cover ($F_{3,497}=6.75$, $P<0.001$), % bare ground ($F_{3,497}=13.45$, $P<0.001$), % cover of ground plants ($F_{3,497}=5.99$, $P<0.001$), and % litter cover ($F_{3,497}=7.75$, $P<0.001$). Jacky Winters used ground substrates with less shrub cover than other species (Table 5). Red-capped Robins and Jacky Winters selected substrates with more bare soil than either Scarlet or Western Yellow Robins (Table 5). The cover of ground vegetation was higher on the substrates used by Scarlet Robins, while Western Yellow Robins selected sites with a high proportion of litter (Table 5).

Initial MANOVA at Durrakoppin found strong differences between the species (Wilks $\lambda_{4,101}=0.86$, $P=0.003$). Univariate tests revealed that these were caused by variation in % cover of ground vegetation ($F_{1,104}=14.65$, $P<0.001$) and % of bare ground ($F_{1,104}=7.03$, $P<0.001$). Red-capped Robins foraged on substrates with more ground vegetation than those used by Jacky Winters (Table 5). Jacky Winter substrates had proportionately more litter and bare soil.

Initial MANOVA at Yellowdine found no sig-

nificant differences between the species (Wilks $\lambda_{4,32}=0.75$, $P=0.054$), but the foraging sites frequented by Red-capped Robins had more shrubs and less litter than where Jacky Winters foraged (Table 5).

Initial MANOVA at Mt Magnet found strong differences between the species (Wilks $\lambda_{4,91}=0.78$, $P<0.001$). This was the result of higher shrub cover at the foraging locations used by Red-capped Robins compared with those used by Hooded Robins ($F_{1,94}=20.78$, $P<0.001$) (Table 5).

4) Intraspecific differences between sites

Initial MANOVA found significant differences between locations for Red-capped Robin (Wilks $\lambda_{16,837}=0.42$, $P<0.001$). Percentage shrub cover ($F_{4,227}=5.96$, $P<0.001$), % bare ground ($F_{4,227}=34.10$, $P<0.001$), % litter cover ($F_{4,227}=33.17$, $P<0.001$), and % ground vegetation ($F_{2,227}=10.05$, $P<0.001$) were significant univariate variables.

Ground foraging substrates used by Red-capped Robins at Durrakoppin had more ground vegetation than all other sites, and there was more ground vege-

tation at Dryandra than Yellowdine (Table 5). The differences in ground vegetation were not significant between Dryandra and the *Acacia* woodland sites, but Yellowdine had less ground vegetation than Gascoyne Junction and Mt Magnet. Shrub cover and the amount of bare soil were greater at Gascoyne Junction and Mt Magnet than at Dryandra and Durrakoppin (Table 5).

An initial MANOVA found significant differences in the attack characteristics of Jacky Winter between Durrakoppin, Dryandra and Yellowdine (Wilks $\lambda_{8,324}=0.70$, $P<0.001$). Percentage shrub cover ($F_{2,165}=9.02$, $P<0.001$) and % ground vegetation ($F_{2,165}=23.14$, $P<0.001$) differed across sites.

The ground foraging substrates used by Jacky Winters at Durrakoppin had greater shrub cover than those at Dryandra and Yellowdine (Table 5). For Jacky Winter foraging sites, ground cover was greater at Durrakoppin and less at Yellowdine than other sites. Correspondingly, the cover of litter and area of bare of soil was greater at Yellowdine (Table 5).

5) Foraging and Habitat Profiles

With the Red-capped Robin at Durrakoppin forming an outlier, there are three distinct groups of woodlands and species; Mt Magnet and Gascoyne Junction (*Acacia* woodlands), Yellowdine (Salmon Gum/Gimlet/Morrel eucalypt woodlands), and Dryandra/Durrakoppin (wandoo eucalypt woodlands) (Fig. 1). Individual species fit more neatly into location groupings than species groupings. That is, different species were more similar in their foraging and habitat pro-

files at the same location than to conspecifics at other locations. Thus, woodland type is more important than species in describing the foraging behaviour of ground-pouncing robins.

DISCUSSION

As with all studies which compare co-existing species within a foraging guild, there were broad overlaps between species in the frequency of foraging manoeuvres, perch heights and foraging substrates (e.g., MacArthur 1958; Recher 1989). However, as shown by Calver and Wooller (1981) and Wooller and Calver (1981a), overlap can be high in some resource dimensions, but when taken together the overlap falls. For this reason, Cody (1974) emphasised the need to consider all resource dimensions together when investigating the competitive relationships among co-existing species. The results presented here considered only resource use during the breeding season and at times when food was likely to be most abundant. Under these conditions, co-existing species may have very similar foraging ecology without necessarily competing for resources (Recher 1989; Wiens 1989). As food becomes less abundant, species become increasingly different in their use of resources (e.g., Recher 1989), a factor not considered in this study.

Despite this limitation, there were significant differences in foraging behaviour between co-occurring species at all sites. Jacky Winters tended to take more aerial prey than other robins, while Western Yellow

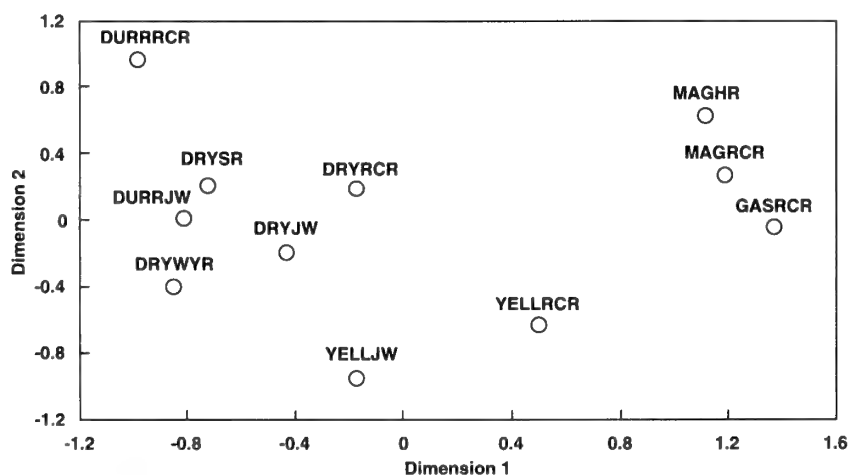


Fig. 1. Multi-dimensional scaling of foraging and habitat attributes for robins at six sites (four in eucalypt woodland and two in acacia woodland). The points are labelled with site and robin species. Sites: YELL (Yellowdine), GAS (Gascoyne Junction), MAG (Mt Magnet), DRY (Dryandra), DURR (Durrakoppin); Species: RCR (Red-capped Robin), SR (Scarlet Robin), JW (Jacky Winter), WYR (Western Yellow Robin), HR (Hooded Robin).

Robins pounced to the ground more frequently than others. Significantly, there was no difference in foraging behaviours between Red-capped and Scarlet Robins at Dryandra, which was the only site where these two species co-occurred. Of the species studied, Red-capped and Scarlet Robins are the most similar in appearance (both are red, black and white), although the Scarlet Robin is half again as large as the Red-capped Robin (Appendix 2).

Despite differences in foraging behaviour, the species studied relied primarily on prey taken from the ground or ground vegetation either by pouncing or snatching. It is therefore necessary to consider other aspects of their foraging ecology to fully appreciate how resources are allocated within this guild.

1) Habitat

While present at the same sites, there were broad habitat differences among the species studied. At Dryandra, Jacky Winters were most common in open Wandoo woodlands with widely spaced large trees and few shrubs. Western Yellow Robins were most often associated with Wandoo and Powderbark Wandoo woodlands on lateritic slopes with a patchy shrub layer to 1.5 m, although they also foraged in open Wandoo woodlands and Mallet *E. astringens* plantations. Red-capped Robins were most common in habitats dominated by sheoak *Allocasuarina* spp. and Jam Wattle *Acacia acuminata*, but also occurred in eucalypt woodlands. Scarlet Robins used Powderbark Wandoo and Wandoo woodlands and frequently occurred in association with Jarrah *E. marginata* and Marri *E. calophylla* which the other species avoided. Most Scarlet Robins were found in habitats with a moderate to dense shrub layer, but they also used Mallet plantations where there is no shrub layer.

The two most similar species at Dryandra, in terms of size, appearance and foraging behaviour, Red-capped and Scarlet Robins, have substantially different geographical distributions. Dryandra is one of the few places where they come into contact (Blakers et al. 1984; Saunders & Ingram 1995; Serventy & Whittell 1951). However, where they came into contact at Dryandra, Scarlet and Red-capped Robins were inter-specifically territorial with Scarlet Robins being dominant (H. Recher unpubl. obs.).

At Durrakoppin, Red-capped Robins were most frequent in mallee (woodlands dominated by multi-stemmed eucalypts) and along the edges of Kwongan shrublands (floristically rich, sandy heathlands). Jacky Winters were restricted to Wheatbelt Wan-

doo/York Gum woodland with a patchy shrub layer. At Yellowdine, Jacky Winters were only found in tall Salmon Gum woodland with an extensive, low (to 1 m) shrub layer and broad open areas. Red-capped Robins were most abundant in Salmon Gum/Gimlet/Morrel woodlands with a shrub layer dominated by *Melaleuca* and *Acacia* species. At Mt Magnet, Red-capped Robins were restricted to dense *Acacia* shrublands, while Hooded Robins occurred in open woodland with widely spaced trees, shrubs and small patches of shrubby woodland. Red-capped Robins were restricted to dense *Acacia* shrublands at Gascoyne Junction, avoiding more open habitats and edges.

Although the three meter radius around foraging perches was too small to fully describe the habitats used by robins, at Dryandra where all species were present, there were significant differences between species in the percent cover of shrubs, ground vegetation, bare ground and litter. These differences largely reflected the different habitat types each species selected. Although less pronounced, similar differences occurred between Red-capped Robin and Jacky Winter at Durrakoppin and between Red-capped and Hooded Robins at Mt Magnet. In each instance, Jacky Winters and Hooded Robins frequented more open habitats than Red-capped Robins. This was also the case at Yellowdine where Jacky Winters and Red-capped Robins co-occurred, but the differences were not significant, possibly because of small sample sizes and the more uniform abundance of shrubs between habitat types.

2) Resource sharing of ground substrates

Within a site, species were more similar to each other in foraging attributes and the foraging substrates selected than they were to conspecifics at other sites. This indicates that potential foraging behaviours were very broad, but their expression was largely determined by the characteristics of the resource, which in this case are the attributes (structure) of the ground surface.

We conclude that co-existence by apportioning ground substrates is not possible within this group of birds. None of the species studied specialised in taking prey from ground vegetation, litter or bare ground. Instead, as described above, species are primarily segregated by habitat and secondarily by foraging behaviour and substrates.

This suggests that the availability (but not necessarily the abundance) of ground-dwelling prey within

the size range taken by these species is limited and likely to be easily depleted in the short-term. For this reason alone, ground-pouncing birds should segregate by habitat, use different foraging behaviours or differ in the size and type of prey when co-habiting. The interspecific territoriality between the Red-capped and Scarlet Robins at Dryandra, and between Scarlet and Flame Robins *P. phoenica* in southeastern Australia (Loyn 1980) is confirmation that very marked differences in size are required between ground-pouncing birds before they can co-exist. Other ground-pouncers, such as butcherbirds and kingfishers, which co-exist with the species studied, tend to be much larger and take many large prey including small vertebrates, use very different foraging behaviours (e.g., sweeping by woodswallows), or are prey specialists (i.e., cuckoos) (Baker & Vestjens 1990; Serventy & Whittell 1951; pers. obs.).

3) Sit and Search

Robins are sit and search predators, but move continually between perches often over long distances. Prey are visually located by a perched bird which then flies or drops to where the prey was seen. The area around a perch in which prey are located is a function of the height of the perch, the openness of the immediate habitat, and the behaviour of the bird. Some of the highest perches and attack distances were at Yellowdine where Jacky Winters and Red-capped Robins obtained a large proportion of their prey by hawking. The greater frequency of hawking also explains the higher perches and longer attack distances for Jacky Winters at Durrakoppin. At Dryandra, where most prey were taken by pouncing to the ground or by snatching prey from ground vegetation or the lower part of tree trunks, perch heights were lower and attack distances for Jacky Winter were smaller. The correlation between perch height and attack distance suggests that high perching birds may search for prey at longer distances, while low perching birds search close to the perch.

The frequent changing of perches, even when prey was taken, supports the suggestion that the availability of ground-dwelling prey is limited and that local resources (those around a perch or set of perches) are quickly depleted.

4) Perch height and prey size

There were differences in the height of perches selected by ground-pouncing robins and the distances at which they located and attacked prey. In particular,

the Red-capped Robin used lower perches and took prey at closer distances than the other robins. Presumably, as the smallest of the species studied, the Red-capped Robin takes the smallest sized prey (for examples of prey size choice, see Calver & Wooller 1981; Hespenheide 1971; Wooller & Calver 1981b) and so must be close to the ground to see them. Furthermore, they do not need to scan a large distance because small arthropods are proportionately more abundant than large ones (e.g., Janzen 1973; Majer & Recher unpubl. data). Larger robins presumably take larger prey and hence need to perch higher and scan larger distances to locate them.

By selecting small prey, Red-capped Robins may be able to exploit closed, shrub habitats more efficiently than the larger species. In turn, this may explain their relative abundance and wide distribution throughout Australia (Blakers et al. 1984). Robins using high perches in the denser habitats where Red-capped Robins are most frequent would have limited lines of sight and thereby be restricted in the area of substrate that could be searched for large prey either on the ground or in the air.

5) Implications for conservation

Many studies in Australia and overseas indicate that bird species assemblages co-exist by partitioning the food resource on the basis of one or more of prey type, foraging height, foraging substrate, or foraging behaviour (e.g., Cody 1974; Ford et al. 1986; MacArthur 1958; Recher 1989; Recher & Davis 1998; Wheeler & Calver 1996; Wiens 1989). If the basis of this partitioning is disrupted (e.g., by changes in available foraging substrates) then the pattern of partitioning could be expected to change, with possible loss of one or more species from the assemblage. Australian studies suggest that such changes have occurred and continue to occur, with past (Burbidge & McKenzie 1989; Recher & Lim 1990) and on-going implications for conservation (Recher 1999; Ford et al. 2001).

Although there were differences in the structure of ground substrates on which different species of ground-pouncers foraged, within a site all species selected foraging sites best described as a mosaic of bare ground, litter and ground vegetation. Disturbances, such as nutrient enrichment, which increase the extent and density of ground and shrub vegetation; frequent burning, which creates an open habitat with increased areas of bare ground and reduced amounts of litter; and, grazing by domestic animals,

which reduces the amount of ground and shrub vegetation (Arnold & Weeldenburg 1998), compacts the soil and increases the amount of bare ground (Abensperg-Traun et al. 2000) will disadvantage ground-pouncers. Among the consequences of these disturbances are decreased abundances and possible changes in the size distribution of terrestrial arthropods favouring smaller species (see Abensperg-Traun et al. 2000; Wooller & Calver 1988).

Such environmental changes appear to be responsible for the decline of ground-foraging birds throughout Australia (Garnett & Crowley 2000; Recher 1999). *Post hoc*, we predict that the impact should be greatest on the largest species of robins; those requiring large prey and relatively large areas of suitable substrate around each perch. This appears to be the case with Jacky Winter and Scarlet and Hooded Robins declining significantly in abundance and distribution throughout their range, while Red-capped Robins persist in relative abundance. Ultimately, however, as degradation of ground substrates in Australia intensifies with continued land clearing, weed invasion and over grazing, all species will be adversely affected. Conservation of this group of birds in Australia requires landscape scale changes in grazing and fire management practices to preserve the foraging resources and ground substrates which this study demonstrates are required by each species.

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Appendix 1. Number of observations of ground-pouncing birds at Dryandra, Durrakoppin and Yellowdine during 1997 and at Gascoyne and Mt Magnet during 1999. Data for Hooded Robin at Dryandra were collected in 1995. The estimated number of different pairs for which we obtained data at each site is shown in parenthesis. Dashes indicate the species was absent from that site.

Location	Bird species				
	RCR	SR	JW	WYR	HR
Dryandra	158 (10)	189 (8)	206 (6)	198 (10)	41 (2) ¹
Durrakoppin	75 (3)	–	86 (3)	–	–
Yellowdine	55 (8)	–	75 (2)	–	–
Gascoyne	69 (12)	–	–	–	–
Mt Magnet	92 (15)	–	–	–	66 (2)

¹ From Recher and Davis (1998).

Appendix 2. Comparative size of Red-capped Robin, Scarlet Robin, Western Yellow Robin, Jacky Winter, and Hooded Robin. Males and females are shown separately for sexually colour dimorphic species. Data are from the Australian Bird and Bat Banding Scheme (Appendix H in Baker et al. 1997). Data are means and standard deviation with sample size in parenthesis.

SPECIES	Measurement		
	Weight (g)	Wing chord (mm)	Tail length (mm)
RCR			
Male	8.6–0.7 (62)	62.9–2.1 (67)	47.7–3.3 (35)
Female	8.7–0.6 (65)	61.5–2.5 (67)	46.5–2.2 (38)
SR			
Male	13.1–1.1 (185)	75–2.2 (108)	55.3–3.3 (31)
Female	13.6–1.5 (99)	73.6–2.2 (78)	55.2–5.2 (19)
JW	15.1–2.5 (30)	86.8–7.2 (29)	60.6–8.5 (19)
WYR	19.0–1.9 (21)	89.3–3.7 (19)	60.6–8.5 (19)
HR			
Male	23.6–2.3 (23)	96.4–3.7 (14)	71.2–1.8 (6)
Female	22.5–1.6 (18)	89.8–2.2 (19)	67.7–2.9 (6)

Heterospecific attraction among forest birds: a review

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Abstract In this paper we review the evidence for a habitat selection process where colonizing individuals use other species presence as cues to profitable breeding sites. Our experimental studies in Fennoscandia and North America have shown that density and species richness of migrant birds breeding in the forests respond positively to experimentally augmented titmice densities. We used analytical modeling to analyze ecological conditions, which may favor a habitat selection process where later arriving individuals (colonists) use the presence of earlier established species (residents) as a cue to profitable breeding sites. We compared the fitness of two colonist strategies: colonists could either directly sample the relative quality of the patches (termed samplers) or, alternatively, they could also use residents as a cue of patch quality (cue-users). Model results suggested that cue-using strategy is more beneficial in most ecological conditions and that this may result in heterospecific attraction. Further field experiments showed that migrant individuals selected nest sites at close vicinity of nesting titmice, and bred earlier and reproduced better. We conclude that heterospecific attraction may be a common and widespread process among forest birds particularly in seasonal environments.

Key words Experimental studies, Habitat selection, Migrant vs. resident birds, Reproductive output, Species richness

Heterospecific attraction was coined by Mönkkönen et al. (1990) to describe habitat selection process where individuals prefer selecting habitat patches already occupied by individuals of another species. It was hypothesized that particularly migrant birds may use residents as cues to profitable breeding sites in conditions where direct and accurate assessing of the quality of available patches is difficult. Short available breeding time and large year-to-year variation in conditions, both characteristics of northern environments, would presumably render heterospecific attraction a profitable habitat selection strategy.

Temperate and boreal passerine bird communities are comprised of resident and migrant species. Residents have to cope with local conditions on a year round basis but migrants are able to avoid the low phases in food availability by migrating elsewhere for the temperate winter. Individuals of many species

show high fidelity to their previous year's breeding territory (Hildén 1965). However, because of high adult mortality approximately half of the individuals in passerine breeding populations are first time breeders who need to make a selection among potential breeding sites. Therefore breeding habitat selection may only be made once in the life of a bird (Cody 1985) stressing the importance of this operation.

Birds obviously use a multiple of cues when selecting breeding sites (Hildén 1965). These include habitat cues, habitat structure, floristics, food resources etc., as well as information on population density (Wiens 1989). Also interactions with other species may influence the occupancy of an area (Cody 1985). The effect of other species on local community diversity may either be positive, such as through heterospecific (see also Slagsvold 1980, Elmberg et al. 1997) or conspecific (Alatalo et al. 1982; Doligez et al. 1999) attraction, or negative through intra- (e.g., Krebs 1971; Fretwell 1972; Mönkkönen 1990) or interspecific (e.g., Reed 1982; Garcia 1983; Gustafsson 1987; Martin & Martin 2001a, b) competition. The presence and density of predators may also decrease the desirability of habitat patches (Mar-

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tin & Roper 1988; Järvinen 1990; Suhonen et al. 1994; Hogstad 1995), if settling individuals are able to actively avoid areas with high risk, as appears to be the case (Norrdahl & Korpimäki 1998).

The idea that individuals prefer to settle close to conspecific individuals at least in some species can be traced back many decades (Lack 1948; Svårdson 1949; Kalela 1952). Stamps (1988) reviewed hypotheses to account for such attraction to conspecific individuals. Aggregated distribution may 1) provide protection against predators by means of communal defence or information delivered by neighbours, 2) benefit an individual if settled neighbours reflect habitat quality, 3) provide social stimulus and hence accelerate or improve breeding performance (e.g. pairing), or 4) improve ability to defend against intruders or competitors. In principle, the three first hypotheses may apply to heterospecific attraction as well. First, it has often been shown that individuals of many species may aggregate to breed in colonies or clumps for protection against nest and other predators (Slagsvold 1980). Second, birds are able to recognize vocalizations of heterospecific individuals, e.g. song (Mönkkönen et al. 1996) and warning calls (Forsman & Mönkkönen 2001; Gunn et al. 2000), and therefore birds can make use of information delivered by other individuals. Aggregations of heterospecific individuals may also provide social stimulus if, for example, females are attracted to such 'hot-spots' of singing males, improving or accelerating pairing.

For heterospecific attraction to operate certain ecological conditions must prevail. First, residents must honestly signal the quality of habitat. This seems a rather robust assumption. Resident birds are very likely less time constrained than migrants, and hence, can invest more time and energy in direct assessing of the relative quality of available habitat patches. Migrant birds are more time constrained in their breeding because in their northern breeding areas habitat selection, pairing, nest building, reproduction, and in some species also moulting has to be fulfilled within just few weeks. Even short delays in the onset of reproduction may accrue severe fitness costs (von Haartman 1967; Alatalo & Lundberg 1984; Harvey et al. 1985; Barba et al. 1995). The presence of resident individuals is likely an honest signal of predation risk in a patch, because residents have had time to evaluate the risk of predation or because residents in risky patches have already fallen victims of predation. Habitat selection and predation result in spatial variation in the density of resident individuals in a land-

scape. Only if such variation existed, would there be potential for migrants to gain information from resident abundance.

Second, migrant bird responding to this variation should be capable of making a choice between different habitat patches. In other words, heterospecific attraction is more likely applied by a species that have to process much information from the landscape before habitat selection, such as habitat generalists apparently have to do (see Dall & Cuthill 1997). Strict habitat specialists more likely respond directly to structural or floristic composition of habitats. Third, for fitness benefits from heterospecific attraction, residents must not cause serious resource depletion for migrants. If severe competition occurs between residents and migrants, migrants should avoid settling in a patch together with residents (Cody 1985). Therefore, heterospecific attraction is more likely among species that do not compete over food and in conditions where food depletion is not a risk (food limitation less severe).

In this paper we first provide some background information on abundances of birds along biogeographic gradients to exemplify the range of conditions where temperate breeding bird communities develop. In particular, we focus on the relative abundance of migrant and resident species in their breeding assemblages, which form the starting point for our later studies on species interactions in forest bird communities. Secondly, we review the evidence, both theoretical and empirical, for heterospecific attraction among forest birds. We consider the effects of this attraction on both breeding numbers and community structure as well as on fitness components of breeding individuals. Finally, we provide a discussion about the generality, importance and conservation implications of heterospecific attraction.

BIOGEOGRAPHICAL PATTERNS IN THE ABUNDANCE OF RESIDENT AND MIGRANT BIRDS AND IMPLICATIONS FOR HETEROSPECIFIC ATTRACTION

A well-known geographic pattern in northern breeding bird communities is the increase in the proportion of migrant birds of the total species and pair numbers with increasing seasonality (MacArthur 1959; Wilson 1976; Herrera 1978; Morse 1989). Usually migrants comprise a larger share of species and individuals in the north than in the south. This geographical pattern is clear, for example, in western Eu-

rope where the proportion of tropical (trans-Saharan) migrants increases from an average less than 10% in the Mediterranean region to about 50% in Fennoscandia (Herrera 1978; for North American pattern, see e.g. Wilson 1976; Morse 1989).

According to Herrera (1978) such a pattern is because carrying capacity of the environment during the severe season (winter) regulates the size of resident species populations below the levels of summer time carrying capacity, which in turn affects the number of migrants that may enter the habitats. In other words, migrants fit in the breeding assemblages in high numbers only where resident populations are regulated to a low level (see also Morse 1989). Resident birds are usually considered superior competitors over migrants and this interspecific competition would keep migrant numbers low in areas and habitats where resident densities are high (Herrera 1978; O'Connor 1981). The pattern of increasing proportion of migrants toward north may also be because of geographical variation in migrant abundance without any linkage to resident abundance. Helle and Fuller (1988), however, showed that total migrant densities do not vary very much from south to north in Europe indicating that the increasing proportion of migrants toward north is mainly due to decreasing resident abundance.

More detailed new analysis by Forsman and Mönkkönen (see Forsman 2000) showed that while resident densities generally declined with latitude migrant densities tended to peak at mid-latitudes (in central Europe) and were lower both further south and north (Fig. 1). The decrease in resident densities was not linear either, and densities north from 60°N were invariably low whereas further south highly variable. The unimodal density pattern of migrants was common to many genera (*Phylloscopus*, *Fringilla*, and *Turdus*) and suggests that migrant densities at geographical scale vary independently of resident numbers. The current evidence, therefore, does not support the conclusion that competition with residents would cause the geographical pattern in migrant proportions, and calls for alternative explanations.

Forsman and Mönkkönen (see Forsman 2000) also analysed the covariation between titmice (resident) and migrant (several genera) densities in Europe after removing the geographical trends in abundances to find out geographic areas where negative (competition) and positive (e.g. heterospecific attraction) associations between residents and migrants are more

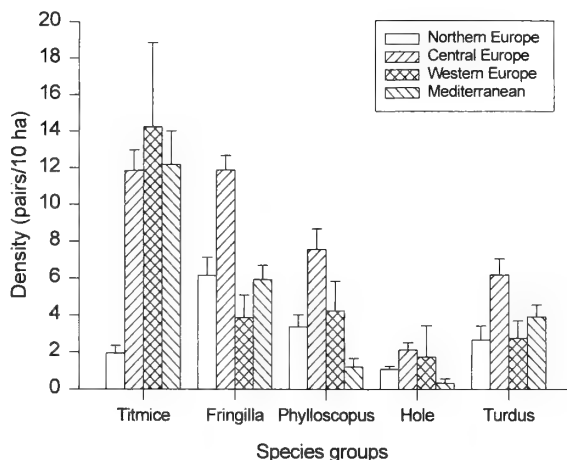


Fig. 1. Density of different forest bird taxa and species groups in different parts of Europe based on published census results (see Forsman 2000). Northern Europe refers to areas north from latitude 60° and southern Europe to areas south from 45°. The area between these latitudes was divided into central Europe (east from 2°E) and western Europe (west from 2°E). Titmice include all European *Parus* spp. and the Long-tailed Tit (*Aegithalos caudatus*). Generic groups refer to all species in the genus, and Hole denotes hole nesting passerine birds other than *Parus* spp. (*Ficedula hypoleuca*, *F. albicollis*, and *Phoenicurus phoenicurus*).

likely than elsewhere. There were many significant positive associations but no significant negative associations. For example, the density of *Fringilla* spp. was positively and significantly associated with titmice densities in northern and central Europe, and that of *Phylloscopus*-warblers in central Europe. This result indicates that positive rather than competitive interactions may prevail between residents and migrants almost irrespectively of the geographic location.

EVIDENCE FOR HETEROSPECIFIC ATTRACTION: NUMERICAL RESPONSES

1) Observational evidence

That birds may be attracted to nest close to other species is a well-known pattern (Durango 1947; Koskimies 1957; Hildén 1964, 1965). Slagsvold (1980), for example, found that Bramblings (*Fringilla montifringilla*) and Redwings (*Turdus iliacus*) preferred to nest in Fieldfare (*Turdus pilaris*) colonies. These species obviously benefited from breeding within Fieldfare colonies because of communal defense against nest predators.

First implications of heterospecific attraction among putative competitor species were found by Reed (1982). He demonstrated that Chaffinch (*Fringilla coelebs*) territories on the mainland of Scotland tended to co-occur with Great Tit (*Parus major*) territories more often than expected by chance alone. In island conditions, however, these two species seemed to compete with each other and occupied non-overlapping territories (Reed 1982). Reed (1982) concluded that the environment on the mainland is richer (more food) than on islands. These results suggest that interspecific interactions may vary considerably according to environmental conditions from competition in situations where resources are limiting (on islands in Reed's case) to positive interactions in others (mainland).

Positive association between territories of two species may also stem from overlapping habitat requirements or from concomitant settling in rich resource. In a playback experiment, where habitat requirements of the species were controlled for, Timonen et al. (1994) demonstrated that two migrants species, the Chaffinch and the Willow Warbler (*Phylloscopus trochilus*), did not avoid settlement near or in resident (*Parus* spp.) territories. Also in this work, there was a tendency that migrants aggregated more than expected at the vicinity of residents. In this experiment, however, food availability was not controlled for and a possibility remained that actually both residents and migrants preferred settling in high quality food patches resulting in positive associations among species.

2) Experimental evidence

To test for numerical response of migrants to resident abundance in their breeding bird assemblages of forest birds we have conducted three rather similar experiments (Mönkkönen et al. 1990, 1997; Forsman et al. 1998). In these studies, we manipulated the occurrence of resident titmice (*Parus* spp.). These manipulations involved winter-feeding and putting up nest boxes to attract titmice on part of the study plots, and removal of titmice from some others. As a result, at the onset of breeding season migrants could make a choice between plots devoid of titmice and plots where titmice densities were augmented. Migrant responses to manipulations were measured by censusing their abundance on experimental plots at the height of the breeding season when breeding pairs possess territories. The experimental design where all plots received both treatments in alternate years ef-

fectively removed any year, food or site related effects on the results (for detailed methodology, see original publications). Heterospecific attraction hypothesis predicts that migrant densities would be higher in plots with titmice than in empty plots.

Our results, encompassing two different continents (Europe and North America) and a variety of conditions from north (Lapland) to south boreal forest zones (Minnesota), were consistent and provided support for the heterospecific attraction hypothesis. The general pattern turned out to be a positive response by migrants to augmented titmice abundance. In all three locations migrant species richness tended to be higher when titmice were present than in absence of titmice (Fig. 2) but this trend was statistically significant only in Lapland. In Lapland and central Finland total migrant abundance responded significantly and positively to augmented titmice abundances, and in central Finland and in Minnesota, foliage gleaners showed a significant positive response. In each area there were one or two individual species showing positive, and none showing negative, response to titmice presence.

The only other study, in addition to our experiments, where the effects of heterospecific attraction on species abundance and community assembly has been addressed is the work by Elmberg et al. (1998) on dabbling ducks. In line with our results, Elmberg et al. (1998) concluded that heterospecific attraction rather than competition affects species co-occurrence in dabbling ducks.

3) Theoretical considerations and a test

Our experiments clearly showed that forest bird species might use each other's presence as cues in breeding habitat selection in a wide variety of environmental conditions. Results from local experimental work, however, do not lend themselves to make far-reaching conclusions about the importance and generality of the heterospecific attraction as a process. Therefore, we used analytical modeling to analyze ecological conditions, which may favor a habitat selection process where later arriving individuals (colonists) use the presence of earlier established species (residents) as a cue to profitable breeding sites (heterospecific attraction) (Mönkkönen et al. 1999). In this model, colonists assessing potential breeding patches could select between high-quality source and low-quality sink patches. Residents occupied a proportion of the source patches. One patch can only foster one pair of colonists. Colonists could

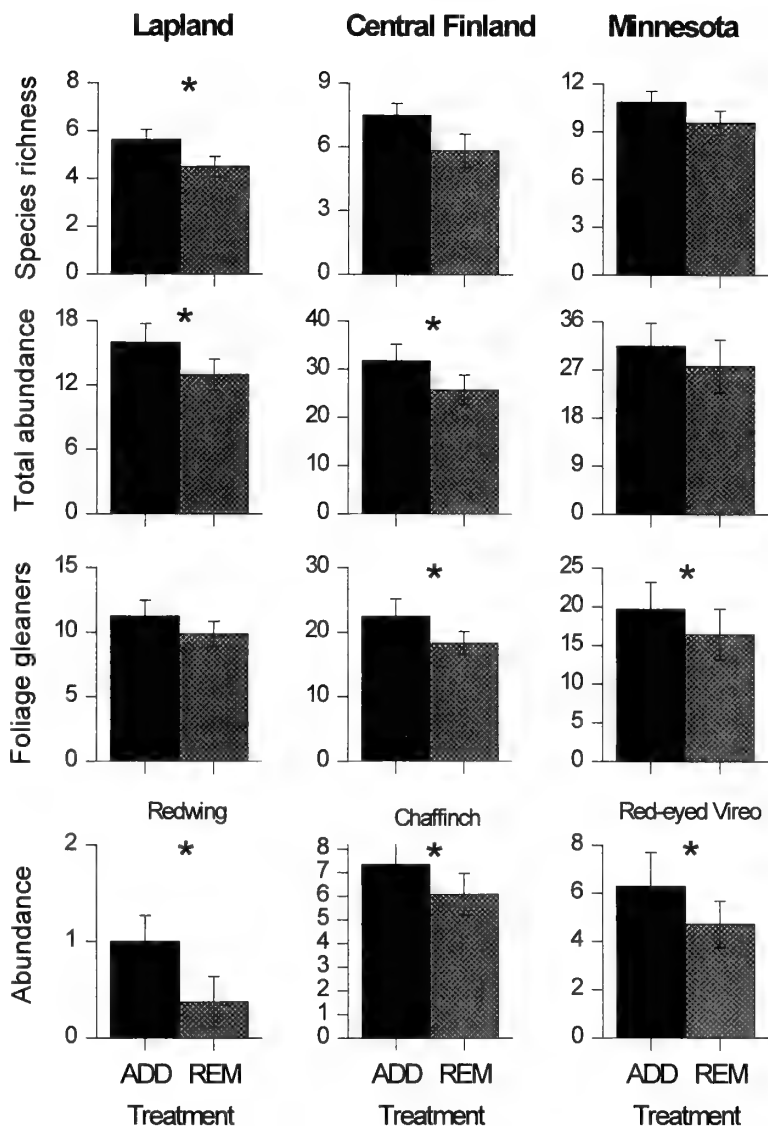


Fig. 2. Mean species richness, mean number of pairs of migrant passerine birds and of foliage gleaning birds in three experimental studies (Lapland, Forsman et al. 1998; Central Finland, Mönkkönen et al. 1990; Minnesota, Mönkkönen et al. 1997). Mean number of pairs for the most strongly responding species is also given (Redwing *Turdus iliacus*, Chaffinch *Fringilla coelebs*, Red-eyed Vireo *Vireo olivaceus*). Error bars denote ± 1 SD. ADD refers to augmented titmice density and REM to removal of titmice from the study plots. Asterisk refers to statistically significant ($P < 0.05$) difference between the treatments.

either directly sample the relative quality of the patches (termed samplers) or, alternatively, they could also use residents as a cue of patch quality (cue-users). Cue-users gained benefit from lowered costs when assessing occupied source patches. We compared the fitness between cue-users and sampler in different ecological conditions and varied, for example, the proportions of sink, empty source and occupied source patches, as well as intensity of competition vs. benefits gained from social aggregations.

We assumed that colonizing individuals use sequential-comparison tactic (SCT) when choosing among patches. It follows from SCT that colonists sample only a limited number of patches (maximum 5 patches). Our model does not result in an ideal distribution because colonists do not necessarily end up selecting the best available patch but the best of the evaluated ones. We used a variant of natural decision theory where sequences can be depicted with decision tree diagrams (for details, see Mönkkönen et al.

1999).

The results of the model indicated that the cue-using strategy is an efficient way to choose the best possible patch both when benefits from social aggregation exceeded the effects of competition (interspecific competition is not strong) but also when interspecific competition is stronger than the benefits (results in avoidance of occupied patches). Samplers can achieve higher fitness than cue-users only if the difference in quality between occupied and unoccupied source patches is low (interspecific interactions weak). This was because the relatively more complicated patch selection procedure of cue-users creates costs, which override the benefits of avoiding the direct assessment of the patch quality, when gains are low. Consequently, cue-using strategy can be used both to avoid competition and to aggregate with heterospecific individuals. Heterospecific attraction would occur whenever colonists gained some benefit from aggregating with residents, which exceeded the effects of competition.

The model also predicted that the strongest attraction to heterospecifics occurs when residents occupy approximately half of high-quality source patches. This is because in such conditions colonists can truly make a choice between empty and occupied source patches. If only few patches are occupied (or empty) chances of finding one are low and choices between empty and occupied source patches are infrequent. In other words, the response of colonists to resident abundance would not necessarily be linear along a whole gradient of resident abundance.

To test this idea we conducted a further experiment in central Finland where resident densities in nine study plot were manipulated create a spectrum of resident densities, relative to previous year's unmanipulated densities (Thomson et al. unpublished). In the first study year titmice were allowed to breed on plots at natural densities, but before the second breeding season their densities were manipulated by feeding, providing nest boxes and removals. Relative changes in migrant densities were analyzed against the difference in titmice densities between years. The hypothesis was that intermediate change in titmice densities would be associated with the highest migrant densities.

The results were only partly consistent with the prediction. There was only very little evidence for a non-linear response. In general the result was a linear response of migrants as shown in Fig. 3 for foliage gleaning guild. This pattern matches well with our

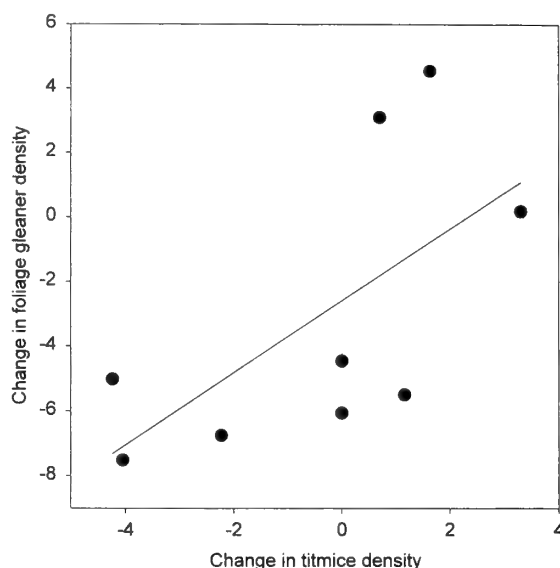


Fig. 3. The change in density of foliage gleaning birds between two consecutive breeding seasons as a response to manipulated titmice density (pairs/10 ha). Titmice densities were decreased (negative change), kept constant, or augmented (positive change) between the years. Foliage gleaners' density significantly increases with increasing titmice density (regression slope = 1.16, $df=7$, $P=0.032$).

earlier experiments and provide further support for heterospecific attraction. The prediction from our analytical model was not, however, confirmed. This is very likely because we did not manage to create high enough titmice densities in our experiment for non-linear responses to emerge. For example, fitting a quadratic curve to density response of the chaffinch in relation to titmice density suggests that the peak in chaffinch density would be achieved when titmice density is about 10 pairs/10 ha. Only after that point would chaffinch densities start to drop with an increase in titmice densities. Maximum densities in our area were about 6 pairs/10 ha, which is rather high density compared to natural densities in the area, but, however, far below the threshold point for non-linear response.

COLONISATION RATES AND FITNESS CONSEQUENCES OF HETEROSPECIFIC ATTRACTION ON DIFFERENT SPATIAL SCALES

1) Habitat selection across scales

Habitat selection of birds is regarded as a hierarchical procedure during which factors affecting decisions of colonizing birds vary considerably (Hutto

1985). On larger scales the influence of individual choice on selection is probably negligible (Hutto 1985) because the choice of geographical area or macrohabitat (e.g., forest type) is quite likely strongly genetically determined (Partridge 1978). However, the smaller the scale is the larger is the number of the characters and cues of the environment that can be taken into account by an assessing individual.

The multitude of different biotic cues affecting habitat selection suggests that perceptual ranges of birds can be very wide and following decisions show considerable behavioural plasticity. Considering the importance of a certain factor in habitat selection, however, it is crucial to take into account the scale where the process takes place and whether or not the selection decisions are adaptive. Cues that are used during the selection process may be either nested across different scales or their effect may take place on one level only. Our earlier work on heterospecific attraction emphasize its effect on habitat patch selection but Timonen's et al. (1994) study suggested that it may operate on smaller scales as well, such as on territory level. To examine the importance of heterospecific attraction in more detail we conducted a set of experiments, which involved two intersecting spatial scales: habitat patches in the landscape and territories within a patch (Seppänen et al. unpublished). In the landscape level we manipulated the densities of resident birds (*Parus* spp.) inhabiting isolated forest patches embedded on an agricultural landscape. In the territory level experiment we studied the settlement of migrant birds in relation to nest of *Parus* spp. In both experiment we used the Pied Flycatcher as a model species.

2) Colonisation rates

If heterospecific attraction is used by Pied Flycatchers (*Ficedula hypoleuca*) when selecting breeding habitat patches, they should first select patches of high titmice density. There was a tendency that Pied Flycatchers preferred high tit density patches to zero density patches. Both the first male flycatcher of each study plot and the average arrival day of males tended to be slightly earlier on high tit density plots than on zero plots, though not statistically significantly (Seppänen et al. unpublished). Female flycatchers had no response whatsoever to the treatments.

On the level of territories Pied Flycatchers were let choose between two nest boxes: the other was close (25 m) and the other one was farther away (100 m) from an active tit nest. If heterospecific attraction is

used at this scale, nest boxes adjacent to a tit nest would be preferred to more distantly located nest boxes. On the territory level, males clearly preferred nest boxes closer to the tit nest to the nest boxes farther away. In 25 set-ups, out of the total 36 cases, males selected first the box closer to the tit nest first. The observed distribution differed significantly from random pattern (1-tailed $P=0.014$ based on resampling). Likewise, females preferred settling to close by nest-boxes to those farther away (23 vs. 12 boxes selected first, respectively; 1-tailed $P=0.043$). It is known that female flycatchers select the nesting site according to the quality of the site and not according to the quality of the male (Alatalo et al. 1986). Therefore, we can consider female preference as independent of male selection even though males arrive first from migration. In this experiment we cannot completely rule out the possibility that both titmice and flycatcher, independently, chose higher quality sites.

3) Fitness consequences

At least equally as important as the scale issue is whether the habitat selection is adaptive or not. Even though heterospecific attraction results in positive association between titmice and migrant densities, it does not necessarily indicate that using heterospecific cues is beneficial in terms of reproductive success (see Pulliam 1988; Martin 1998). We tested if heterospecific attraction results in an increased fitness in the Pied Flycatcher by comparing reproductive success in patches where tits nested with patches devoid of tits using the abovementioned experimental arrangement.

In general, the presence of titmice had a positive effect on the reproductive success of the Pied Flycatcher (Seppänen et al. unpublished). Flycatchers were able to start egg-laying earlier, and the time delay from the female arrival to the first egg was on average 1.7 days shorter in patches where tits were present than in patches devoid of tits. Moreover, nestlings hatched 1.7 days earlier, and there were on average 0.6 more nestlings in broods in patches with tits than in patches without tits. Fledglings growing up in the neighborhood of titmice were larger than in the nests farther away.

The results of these two experiments clearly indicate two things. First, heterospecific attraction seems to be an adaptive habitat selection strategy in terms of reproductive success in the Pied Flycatcher. Second, the effect of heterospecific attraction on habitat selection and fitness is potentially working on two over-

lapping scales; the presence of tits is first used in roughly comparing the quality of habitat patches at the landscape level followed by a more fine-tuned small scale nest site selection with preference to neighborhood of tit nest sites (see also Timonen et al. 1994). The results of the experiments also provide an example of nested habitat selection across scales with possibly cascading effects from titmice presence in the landscape in terms of higher occupation rates and reproductive success.

DISCUSSION

To summarize, boreal forest environment provide an example of a system where using resident species as cues is a profitable strategy in the breeding habitat selection of migrant birds. The experiments conducted on two continents indicate that heterospecific attraction of migrants to titmice increase the diversity and total abundance in local breeding communities. Migrant birds apparently use titmice abundance in comparing the relative quality (food and/or predators) of habitat patches. Our work at the biogeographic scale suggests that heterospecific attraction might not be restricted to boreal conditions but may be a wide spread process in forests bird communities. Analytical modeling approach suggested that this sort of cueing from residents in most cases creates fitness benefits and is therefore selected for. This was further shown in experiments on titmice and Pied Flycatchers. We observed that flycatchers preferred areas of high tit density in their settlement and, moreover, their reproductive success was higher in patches with tits than without them.

Recent theoretical study has suggested that positive interspecific interactions are plausible, common and intensive in a wide variety of environmental conditions. For example, Dodds (1988) showed that in highly seasonal ("boom and bust") environments, positive interactions, such as facilitation and mutualism, are selected for. Similarly, Bertness and Callaway (1994) suggested that positive interactions should be particularly common in communities under a severe physical stress (e.g., in highly variable or seasonal environments) and/or experiencing high consumer (predation) pressure. Bird communities in temperate and particularly in boreal settings occur in conditions that very likely meet these conditions: seasonality is pronounced producing a large difference in resource levels between summer and winter (Blake et al. 1994) and predation pressure on adults, nests and

young birds is heavy (Hanski et al. 1996; Solonen 1997).

We were able to show fitness benefits for Pied Flycatchers from settling in patches with titmice, but many earlier studies, conducted further south in temperate forests, have also shown competitive interactions between flycatchers (Pied Flycatcher or Collared Flycatcher, *F. albicollis*) and tits (Slagsvold 1975; Sasvari et al. 1987; Gustafsson 1987, 1988; Merilä & Wiggins 1995). For example, Gustafsson (1987) showed that tits affected negatively the fitness of collared flycatchers. Potential reason for these seemingly contradictory results is in the difference in densities of residents among studies. In these southern studies titmice densities have usually been 2–5 times higher than the highest densities in our study areas (4–5 pairs/10 ha). Contrasting results in our and Gustafsson's (1987) study suggests that interspecific interactions may change along with different densities of potential competitors. This matches well with the results of our analytical model, which predicted stronger attraction to residents at intermediate abundance (see above).

The results of the experimental studies indicate that birds' readiness to follow heterospecific cues varies among places and species. Not all species responded positively to increasing resident densities in our experiments, and there obviously is much variation in within-species responses to resident densities according to local conditions. In what conditions are species more apt to using heterospecific cues? Young birds selecting their first nesting sites are very likely more susceptible to use heterospecific cues than older individuals, which usually return to their previous year's breeding site. Young birds might also be better off by using heterospecific residents than conspecific as cues because the presence of conspecifics may not reflect relative quality of the breeding sites in the current year but rather conditions in the past when site selection was made. Given the extensive between-year variation in conditions taking one's cue from residents is quite likely more beneficial. It follows that the intensity of heterospecific attraction should vary according to the proportion of young individuals in the breeding population. We earlier referred to habitat generalists as being a species group apt to heterospecific attraction because they are not very tightly dependent on any particular habitat feature. In two Finnish experiments (Mönkkönen et al. 1990; Thomson et al. unpublished), we found that the Chaffinch, an acknowledged habitat generalist,

showed the strongest response to increased titmice density. In the northernmost experiment (in this area the Chaffinch is relatively few in number) the Brambling had also a positive response to augmented tit densities (Forsman et al. 1998). Brambling is also a habitat generalist and, in addition, does not show site-fidelity to previous year's breeding sites (Enemar et al. 1984; Mikkonen 1983). Brambling is therefore free to use external cues in order to find as good breeding habitat as possible.

The results of the experiments on Pied Flycatcher provide also some evidence about the processes behind the heterospecific attraction. We have earlier suggested that the presence and density of tits is used to make quick assessment of relative quality among habitat patches in the landscape. Our results showed, that indeed, high tit density patches and nest boxes closer to the nest of tit were colonized earlier indicating that tits were used as a measure of the patch and site quality resulting in increased fitness. Female flycatchers in patches where tits were present showed shorter time lags between arrival and the onset of egg-laying. Pied Flycatchers, as many other birds, are time constrained in their breeding and an early start of the breeding has a positive effect on the reproductive output (e.g., von Haartman 1967; Lundberg & Alatalo 1992). Our results also suggest that flycatchers may also benefit from the tits through enhanced feeding efficiency or predator vigilance.

At the landscape level, heterospecific attraction results in a clumped distribution of individuals and species, a common pattern in nature (Hanski et al. 1993). This would explain the common observation that some seemingly suitable habitat patches remain empty. If colonization of patches is more generally dependent on the presence of individuals of other species, this would further complicate population dynamics in patchy landscapes. For example, metapopulation models, for the sake of realism, should incorporate interspecific interactions such as heterospecific attraction. Given the increasing fragmentation of landscapes taking interspecific interactions into account when assessing individual dispersal and population viability is becoming increasingly important. For example, many old-forest associated resident species in Fennoscandia show declining population trends because of habitat loss and fragmentation (e.g. Haila & Järvinen 1990). This may have negative effects on migrant species as well, if colonization rates in remaining patches depend critically on heterospecific cues.

Our experiments focused only on migrant birds' habitat selection and fitness, and provided no evidence of whether heterospecific attraction results in a mutualistic relationship where also residents benefit from migrants' presence or benefits are asymmetric accruing only to migrants. This remains as a challenge for future studies. The experiments in temperate forests have so far encompassed only the high end of the resident density gradient; resident densities in nest-box studies may be unnaturally high compared to natural densities (e.g. Wesolowski et al. 1987). It would be interesting to see results from an experiment similar to our flycatcher work conducted in temperate settings where numerical response and fitness effects were studied over the whole gradient of resident densities. These results would further test for the importance and intensity of interspecific interactions (both negative and positive) and even reveal threshold conditions where originally positive interactions turn into negative ones.

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The effect of a typhoon on the flocking and foraging behavior of tits

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Abstract A typhoon, that struck Kyushu, the southernmost of the four main islands of Japan, in September 1999, causing extensive wind damage to forests, was found to have affected the flocking and foraging behavior of Varied *Parus varius* and Great Tits *P. major*. After the typhoon had passed, the tits tended to participate in mixed-species flocks and preferred to forage in the lower parts, rather than in the upper parts, of the trees. Also the proportion of plant products in the diet of the Varied Tit was reduced. The population and average flock size of the tits, however, remained stable even after the typhoon. The abundance of plant products as food resources remained unchanged despite severe damage to the trees, but the vegetation cover was reduced, which probably increased the predation risk. The increase of mixed-species flocking may have resulted from the increased risk of predation; mixed-species flocking is thought to increase vigilance and foraging efficiency while not increasing intraspecific competition. Changes in diet and preferred foraging sites were also consistent with the increased predation risk hypothesis. We conclude that the changes in foraging and flocking behavior after the typhoon were mainly due to the increased predation risk caused by the reduced vegetation cover.

Key words Foraging site, Forest disturbance, Tit, Typhoon, Winter flocking

Disturbance by storms is among the most important factors in determining the structure and species composition of forest biotic communities (White 1979; Tanner et al. 1991). Bird populations are also affected by storms, both directly as a result of the stress of storms and indirectly as a result of habitat modification (Askins & Ewert 1991; Lynch 1991; Waide 1991; Wunderle et al. 1992). Although many studies have reported on the population dynamics of birds after storms, little attention has been paid to their behavioral response.

In Kyushu, the southernmost of the four main islands of Japan, typhoons are the most significant agent of forest disturbance (Yamamoto 1992). The passage of a powerful typhoon through Kyushu in 1999 provided us with a rare opportunity to document the effects of a storm on avian behavior. The aim of this paper is to describe the effects of this severe typhoon on the flocking and foraging behavior of the Varied Tit *Parus varius* and the Great Tit *P.*

major. Various factors affecting avian flocking and foraging behavior previously have been revealed, including: food abundance (Berner & Grubb 1985; Székely et al. 1989; Kubota & Nakamura 2000), weather conditions (Ekman 1984; Grubb 1987; Nakamura & Shindo 2001), inter- and intraspecific competition (Ekman 1987; Alatalo & Moreno 1987), abundance of congeneric species (Matthysen 1990), predator abundance (Suhonen 1993; Kullberg 1998), and the distribution of protective cover (Krams 1996). Despite the number of these studies, few have examined the effects of storms. To reveal the impact of the typhoon we compared the diets, foraging heights, and mixed-species flock attendance of the two species between the winters preceding and following the typhoon.

STUDY AREA AND METHODS

The study was carried out at Tatsutayama Experimental Forest in Kumamoto, Kyushu, Japan (32°49'N, 130°44'E, 28.4 ha, 48–152 m asl). Tatsutayama is an isolated hill forest area of about 450 ha,

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and the Experimental Forest is located on the southwestern slope of the hill. It is mostly covered with secondary evergreen broad-leaved forests 40–50 years of age, with some small coniferous plantations. The dominant tree species in this secondary forest is *Castanopsis cuspidata*, with an average height of about 17 m.

On 24 September 1999, a severe typhoon (9918 Bart) struck Kyushu and its eye passed within 40 km of the Experimental Forest moving at 40 km h^{-1} , with a pressure at the eye of 945 hPa. At the Kumamoto Local Meteorological Observatory, 2.5 km west of our study site, a wind speed of over 10 m s^{-1} was recorded for seven hours, with a maximum speed of 49.0 m s^{-1} (Japan Meteorological Agency 1999).

To examine the structural damage caused to trees by typhoon 9918 Bart, we established five $2 \text{ m} \times 50 \text{ m}$ transects within which we measured all the trees above breast height, and categorized the trees into three groups: 1) Sound; mostly healthy with slight or little defoliation; 2) Injured; trunk broken, trunk leaning, trunk down, limbs broken, or severely defoliated, and 3) Dead; died within two years of the typhoon.

To examine the effect of the typhoon on the population and flocking behavior of tits, we conducted annual bird censuses from 15 November to 31 December, from 1996 to 1999. Since the number of tits and their flocking and foraging behavior change continuously throughout the year, we confined the study to this short period when the social organization of tits is relatively stable (Saitou 1978; Gosler 1993; Kubota & Nakamura 2000). Moreover, since we could not find an appropriate control site, we compared the data sets from the four years defining the three years 1996–1998 as control years and 1999 as a disturbed year. To reduce the possibility of misidentifying the ‘among-year-fluctuation’ to be an effect of the typhoon, we regarded only those values in 1999 that were significantly different from those of the other three years, as having been disturbed by the typhoon. Although some typhoons affect our study site every year, no severe typhoons with maximum wind speeds of over 40 m s^{-1} were recorded in the control years nor during the five years prior to the research.

An elliptical, 3.8 km, census route was established in the study site, and this was surveyed six times each year between 0730 and 1030. The species and number of all birds observed within 25 m on either side of the route were recorded. We carefully avoided repeated counts of the same flock. Since the vegetation was not dense in our study site, we assumed that de-

tectability within 25 m of the transect line was high and constant, and that the number of tits recorded within the area reflected their relative densities.

Each tit encountered was categorized as either participating in a mixed-species flock, in a mono-specific flock, or as being solitary. Three criteria were used to define a flock: (1) all members remain within about 20 m of each other; (2) flock members remain together for at least three minutes, and (3) members move at least 30 m in the same direction. When more than two birds of two species were associating together, they were defined as a mixed-species flock, following Bell’s definition (1986).

In our study area, in addition to Paridae other species were also recorded as participating in mixed-species flocks. These included: Long-tailed Tit *Aegithalos caudatus*, Japanese White-eye *Zosterops japonicus*, Japanese Pygmy Woodpecker *Dendrocopos kizuki*, Goldcrest *Regulus regulus*, Ashy Minivet *Pericrocotus divaricatus*, Red-flanked Bushrobin *Tarsiger cyanurus*, and Japanese Bush Warbler *Cettia diphone*.

It was not possible to determine the social organization of the Varied and Great tits in detail, since individual were not marked, therefore, we used the term ‘mono-specific units’ to describe the basic social organization that included solitary individuals, mono-specific flocks, and the same species members belonging to mixed-species flocks. Mixed-species flock attendance rate was calculated for each species as the proportion of individuals attending the mixed-species flocks in relation to the total number of individuals observed.

To examine the effects of abiotic factors, we compared the weather parameters on census dates in the control and disturbed years, daily average temperature and wind velocity, recorded at the Kumamoto Local Meteorological Observatory. These data were provided by the Japan Meteorological Agency.

We recorded the diet and the foraging heights where successful foraging attempts by tits were observed, from November to January each year. Foraging heights were divided into four categories: (1) upper layer ($>12 \text{ m}$), (2) middle layer (6–12 m), (3) lower and shrub layers (0–6 m), and (4) on ground. Unfortunately, we could not divide these observations according to whether or not birds attended mixed-species flocks, because we recorded foraging behavior independently of the bird censuses.

The abundance of acorns and other seeds was estimated using litter traps. Ten round traps, each with an

opening of 0.58 m², were placed in the *C. cuspidata* forest and we collected the contents over the three winter month of November, December and January. We sorted out seeds and mature acorns from the contents, oven-dried (70°C, 72 h) and weighed them. Small immature acorns were excluded from the abundance measurement, since tits seldom fed on them (Higuchi 1975).

We used the Kruskal-Wallis test to analyze the flock size data. To evaluate the differences among groups, we employed Dunn's procedure following Zar's manual (1999). We simply used chi-square test (contingency table) to analyze if the mixed-species flock attendance, foraging sites, and food items were independent of year, because our sample sizes were large enough to use this test without correction in most cases. When those variables were not independent of year, we then evaluated the contribution of each cell of the contingency tables using adjusted residuals (d_{ij}), which are approximate to z scores (Everitt 1977).

RESULTS

1) Disturbance by the typhoon

After the typhoon passed, 8.4% of the trees above breast height died and 28.2% were severely injured (their limbs and/or trunks were broken, or they were uprooted; see Table 1). The wind damage to the canopy was greater than that to the sub-canopy, 13.6% of the canopy trees (with a diameter at breast height of over 20 cm) died and 72.7% were severely damaged (Table 1).

Most of the trees in our study site were extensively defoliated by the strong typhoon winds, and annual litter fall in 1999 was 1.3- to 2.0-fold greater than during the three years prior to the typhoon (Sato unpublished). As a result of this destruction, the average canopy cover was reduced from 95.4% to 87.2% (Saitou, S. personal communication). We have only limited information on the winter predation risk relating to this decrease of cover. The mortality of young

birds, however, was higher during the breeding season following the typhoon than in the preceding seasons. For example, 52.3% of young Great Tits disappeared within two weeks after fledging in 2000, whereas only 28.6% had disappeared in 1997 (chi-square test, $\chi^2=5.55$, $df=1$, $P=0.019$). We also observed several attacks on family flocks of Great Tits in 2000, but not in other years. These attacks included three by Jungle Crows *Corvus macrorhynchos* (one was successful), and one successful attack by a Japanese Lesser Sparrowhawk *Accipiter gularis* (Seki unpublished).

Despite the severity of the habitat modification resulting from the passage of the typhoon, the differences among years were not significant for either temperature or wind velocity (Table 2).

2) Number of tits

The number of individual Varied Tits recorded did not differ significantly among years (Table 3). The number of Great Tits observed in the three years 1997, 1998 and 1999, did not differ significantly, although the number of birds seen in 1996 differed significantly from the number in 1999 (Dunn's procedure, 1996 vs 1999, $Q=3.50$, $P<0.005$; 1997 vs 1999, $Q=1.00$, $P>0.50$; 1998 vs 1999, $Q=0.65$, $P>0.50$).

3) Size and composition of flocks

Neither the size of mono-specific units, nor the size of mixed-species flocks containing each species of tit, differed among the four years for either tit species

Table 1. Structural damage to trees in the study area caused by typhoon 9918 Bart. Figures show the number of trees in each category.

DBH class (cm)	<10	10-20	20-30	30-40	>40
Sound	226	9	5	1	
Injured	61	14	24	6	2
Dead	18	8	4	2	

Table 2. Weather parameters on census dates recorded at the Kumamoto Local Meteorological Observatory (mean \pm SD). Data were provided by the Japan Meteorological Agency, through the database of the Computer Center for Agriculture, Forestry and Fisheries Research.

	1996	1997	1998	1999	F	P
Temperature (°C)	7.7 \pm 3.3	9.1 \pm 4.9	8.4 \pm 2.4	5.8 \pm 3.9	0.83	0.50
Wind velocity (m/s)	1.6 \pm 0.3	1.9 \pm 0.6	1.6 \pm 0.2	2.1 \pm 0.4	2.24	0.12

Table 3. Comparison of observed number of individuals and the size of flocks in the control years and in the year disturbed by the typhoon (mean \pm SD).

Species		Year	Number of individuals (per census)	N ¹	Size of mono-specific units ²	N ³	Size of mixed-species flocks ⁴	N ³
a) Varied Tit	Control years	1996	23.8 \pm 8.6	6	2.6 \pm 1.8	55	16.7 \pm 9.8	10
		1997	24.2 \pm 3.6	6	2.1 \pm 1.1	69	8.1 \pm 5.2	14
		1998	18.2 \pm 3.2	6	2.1 \pm 1.2	52	9.4 \pm 6.0	11
	Disturbed year	1999	18.8 \pm 3.5	6	1.9 \pm 0.8	59	11.0 \pm 10.0	30
		Kruskal-Wallis test (df=3)	Hc=6.48 P=0.09		Hc=4.77 P=0.19		Hc=5.15 P=0.16	
b) Great Tit	Control years	1996	6.5 \pm 1.4*	6	1.5 \pm 0.8	26	11.9 \pm 9.9	14
		1997	15.3 \pm 3.7	6	1.7 \pm 0.8	54	9.1 \pm 5.2	19
		1998	16.2 \pm 1.7	6	1.9 \pm 1.0	51	12.6 \pm 9.6	17
	Disturbed year	1999	19.3 \pm 6.2	6	2.0 \pm 1.0	59	10.6 \pm 9.7	36
		Kruskal-Wallis test (df=3)	Hc=14.04 P=0.003		Hc=5.65 P=0.13		Hc=1.32 P=0.72	

¹ Frequency of census² We used the term 'mono-specific units' to mean a basic social organization, including solitary individuals, mono-specific flocks, and the same species members belonging to mixed-species flocks.³ Number of observed units or flocks each year⁴ Size of mixed-species flocks containing each species of tit that also include the number of species other than tits: Long-tailed Tit, Japanese White-eye, Japanese Pygmy Woodpecker, Goldcrest, Ashy Minivet, Red-flanked Bushrobin, and Japanese Bush Warbler.* Significant difference from 1999 ($P < 0.05$, Dunn Procedure).**Table 4.** Mixed-species flock attendance rates (%) in the control years and in the year disturbed by the typhoon.

	Control years						Disturbed year		χ^2 -test		
	1996	N ¹	1997	N ¹	1998	N ¹	1999	N ¹	df	χ^2	P
Tits											
Varied Tit	30.8	143	23.4	145	17.4	109	52.2	113	3	37.26	<0.001
Great Tit	59.0	39	31.9	92	36.1	97	68.1	116	3	38.45	<0.001
Long-tailed Tit	50.8	252	48.3	201	56.6	234	91.1	169	3	89.00	<0.001
Other species											
Japanese White-eye	10.4	554	12.8	240	11.7	358	35.3	292	3	91.63	<0.001
Japanese Pygmy Woodpecker	23.3	47	34.0	60	34.8	46	51.7	58	3	10.51	0.015
Goldcrest	22.2	2	0.0	9	57.1	14	100.0	11		—	—
Ashy Minivet	0.0	19	10.5	20	0.0	12	13.3	15		—	—
Red-flanked Bushrobin	0.0	44	2.3	42	2.2	45	5.7	35		—	—
Japanese Bush Warbler	0.0	55	0.0	77	1.3	76	0.0	85		—	—

¹ Sample size (N) shows the total number of individuals observed each year.

(Table 3).

The mixed-species flock attendance rate of the Great Tit was always higher than that of the Varied Tit within each year, even in the disturbed year (Table 4). The mixed-species flock attendance rate in 1999

was higher than in the three control years, not only for both *Parus* species but also for the Long-tailed Tit, the Japanese White-eye and the Japanese Pygmy Woodpecker (Table 4). The results in 1999 contributed most to the dependence on year in all these

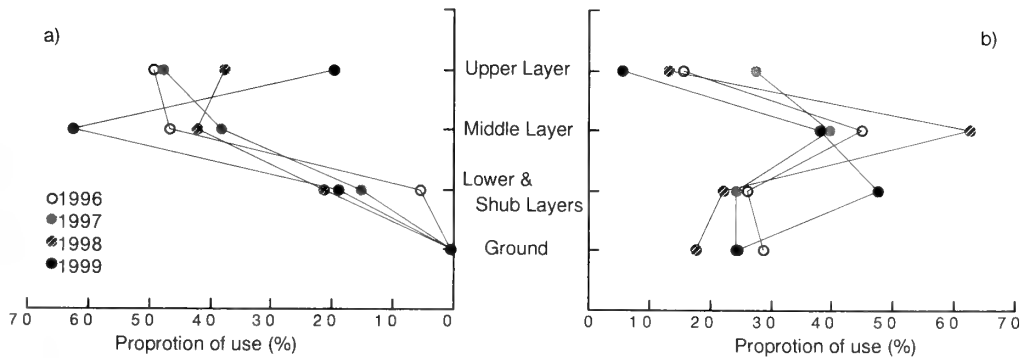


Fig. 1. The foraging heights of a) Varied Tit and b) Great Tit in the control years and in the year disturbed by typhoon 9918 Bart. The observed frequency of feeding attempts each year is shown in Table 5.

species (adjusted residuals, Varied Tit, $d_{\text{mixed}, 1999} = 5.65$, $P < 0.001$; Great Tit, $d_{\text{mixed}, 1999} = 5.45$, $P < 0.001$; Long-tailed Tit, $d_{\text{mixed}, 1999} = 9.06$, $P < 0.001$; Japanese White-eye, $d_{\text{mixed}, 1999} = 9.54$, $P < 0.001$; Japanese Pygmy Woodpecker, $d_{\text{mixed}, 1999} = 2.92$, $P = 0.004$). For the other four species, we could not perform statistical analyses, because the number of individuals participating in mixed-species flocks was too small. Although we do not have quantitative data on the leader-follower relationships in the mixed-species flocks, if Long-tailed Tits were present they usually led the flock. In those flocks without Long-tailed Tits, we did not find any tendency for the Varied Tit or the Great Tit to be the leader (Seki, pers. obs.).

4) Foraging heights

Varied Tits were only observed foraging in trees and never on the ground during the study period (see Fig. 1). The observed frequency of each forest layer used was not independent of year in the Varied Tit (chi-square test, $\chi^2 = 27.31$, $df = 6$, $P = 0.001$). After the typhoon's passage, the Varied Tit foraged significantly less in the upper layer and significantly more in the middle layer instead (adjusted residuals, upper layer, $d_{\text{upper}, 1999} = -4.48$, $P < 0.001$; middle layer, $d_{\text{middle}, 1999} = 3.29$, $P = 0.001$; lower and shrub layer, $d_{\text{lower}, 1999} = 1.47$, $P = 0.14$). The Great Tit also foraged less in the upper layer after the disturbance and shifted to the lower part of the trees, although the effect of year was not significant (chi-square test, $\chi^2 = 15.12$, $df = 9$, $P = 0.09$).

5) Diet components

In our research area, plant materials accounted for 47.3 to 53.5% of the Varied Tit's diet in the control years, whereas the proportion of plant materials in the diet decreased to 30.1% in the disturbed year (Table

5). Since unspecified items were assumed to be invertebrates (on the basis of the foraging site), we divided their diet into two parts, plant diet, and non-plant diet. The observed frequency of each group foraged was not independent of year (chi-square test, $\chi^2 = 12.33$, $df = 3$, $P < 0.001$), and the results in 1999 contributed most for the dependence on year (adjusted residuals, $d_{\text{plant}, 1999} = -3.43$, $P < 0.001$).

The Great Tit also fed on plant products although the proportion was not high (Table 5). The Great Tit seldom ate acorns, probably because of physical constraints. In fact, we observed only two incidences of Great Tits eating acorns, in both cases they were broken due to drying. The diet composition of the Great Tit was independent of year during the study period (chi-square test, $\chi^2 = 1.09$, $df = 3$, $P = 0.78$).

6) Plant abundance

The abundance of plants, especially acorns, was highly variable among years (Table 6). Although acorns and seeds were not abundant in 1999, the abundance was still greater than that of the previous winter, which was one of the control years undisturbed by severe typhoons.

DISCUSSION

We observed three changes in tit behavior after the severe disturbance caused by the typhoon. First, attendance rate in mixed-species flocks increased after the disturbance compared with the previous three years. Secondly, the proportion of plants in the Varied Tit's diet was reduced, although there was no change in the Great Tit's diet. Finally, the tits tended to prefer the lower part of the trees to the upper part as their foraging sites. The population and average flock size of the tits, however, were rather stable in spite of the

Table 5. Annual variation in the winter diet (%) of Varied and Great Tits from 1996-1998.

		Varied Tit				Great Tit			
		Control years			Disturbed year	Control years			Disturbed year
		1996	1997	1998	1999	1996	1997	1998	1999
Plant materials									
	Acorns	37.5	24.3	27.9	19.4	4.5	0.0	0.0	0.0
	Seeds	15.0	23.0	25.6	10.7	6.8	7.9	15.4	9.2
Non-plant materials									
Invertebrates									
	Caterpillars	12.5	10.8	14.0	11.7	20.5	15.8	19.2	20.0
	Pupae	2.5	5.4	0.0	4.9	2.3	18.4	7.7	4.6
	Spiders	1.3	1.4	2.3	1.9	2.3	10.5	7.7	9.2
	Lepidoptera(adults)	0.0	1.4	0.0	1.9	4.5	2.6	11.5	3.1
	Hemiptera	1.3	1.4	0.0	1.9	0.0	5.3	3.8	3.1
	Coleoptera(adults)	0.0	1.4	2.3	5.8	0.0	0.0	0.0	3.1
	Diptera(adults)	0.0	1.4	0.0	2.9	0.0	2.6	3.8	1.5
	Hymenoptera(adults)	0.0	0.0	0.0	0.0	2.3	0.0	0.0	1.5
	Other Invertebrates	12.5	5.4	7.0	8.7	31.8	10.5	11.5	12.3
Unspecified		17.5	24.3	20.9	30.1	25.0	26.3	19.2	32.3
Total number of items		80	74	43	103	44	38	26	65

Table 6. Abundance (kg ha^{-1}) of acorns and other seeds in the control years and in the year disturbed by the typhoon.

		Acorns	Other seeds
Control years	1996	456.77	1.66
	1997	75.92	1.91
	1998	1.64	1.34
Disturbed year	1999	4.38	1.43

extensive habitat modification.

Foraging and flocking decisions are very sensitive to biotic and abiotic environmental changes (Matthysen 1990); since small passerines suffer from energy shortages during the cold and short winter days (Jansson et al. 1981), they always face a trade-off between the benefit of efficient foraging and the cost of predation risk when they make behavioral decisions (reviewed in Lima & Dill 1990; Matthysen 1990; Suhoonen et al. 1993). Based on previous studies dealing with wind disturbance (Askins & Ewert 1991; Engstorm & Evans 1990; Grant et al. 1997; Lynch 1991; Waide 1991; Wunderle et al. 1992), we had expected two major environmental changes: fluctuation of food abundance and the decrease of vegetation cover.

Fluctuations in food abundance, however, are unlikely to have caused the behavioral changes in the present study. Although the strong typhoon winds in

1999 blew off large numbers of immature acorns and seeds (Sato unpubl.), the production of mature acorns and seeds during the following winter was still greater than that of poor crop years, such as 1998 (Table 6). The seed production of tree species in general is highly variable between years regardless of the effects of wind storms (Higuchi 1975; Kelly 1994). In 1998, Varied Tits selectively ate acorns despite their low abundance, but did not do so in 1999. Neither Great Tit nor Varied Tit increased their mixed-species flock attendance rate in 1998, but in 1999 they did. The decrease of plant products after the typhoon seems unlikely to be the cause of behavioral changes of tits. Furthermore, potential invertebrate prey for tits did not markedly increase or decrease even in the disturbed winter. Increases in invertebrates, which might have caused the Varied Tit to alter its diet, have often been reported after storms, but usually occur from spring following the damage (Thompson 1983; Furuta et al. 1984). Decreases in invertebrates, which might happen after canopy destruction and thus lead to mixed-species flocking, could not have been so severe in the study area, because Varied Tits risked shifting their diet from plant products to invertebrates in the disturbed winter.

Reduced cover could have caused the observed behavioral changes as a result of the increased risk of predation (Engstorm & Evans 1990; Thiollay 1997;

Grant et al. 1997). The reduced degree of vegetation cover was observed also in our study area, and it continued throughout the winter, since refoliation and sprouting could not proceed so rapidly in warm temperate forests (Bellingham et al. 1996). Although we have only limited information on the winter predation risk, the increased mortality of young during the breeding season after the typhoon would support our increased predation risk assumption.

Higher predation risk increases the mixed-species flock attendance rate (Székely et al. 1989; Ekman 1989; Matthysen 1990; Suhonen et al. 1993), because heterospecific flocking is assumed to increase vigilance and foraging efficiency but does not increase intraspecific competition (reviewed in Lima & Dill 1990; Bednekoff & Lima 1998). Moreover, since individuals in heterospecific flocks are probably not influenced by long-term social bonds, interspecific associations are more sensitive than intraspecific associations to environmental changes (Matthysen 1990), such as the disturbance caused by a typhoon. Our findings, that mixed-species flocking increased once vegetation cover had been reduced, were consistent with the increased predation risk hypothesis. The average size of mixed-species flocks in 1999 did not increase in spite of the increased mixed-species flock attendance rates, presumably because of the smaller size of mono specific units of the Long-tailed Tit, nuclear species for mixed-species flocks (averaging 7.4 in 1999 and 7.9–12.0 during 1996–98).

Predation risk also affects the diet of prey species. Numerous studies have demonstrated that the presence of predators increases the proportions of prey items found and consumed in a safer place with a safer method (Lima 1988a; Lima 1988b; Suhonen 1993; Suhonen et al. 1993; Krams 1996; Kullberg 1998, to name a few). The Varied Tit preferred the acorns of *C. cuspidata* before the disturbance, since other species did not take it in spite of its high energetic efficiency. However, acorns have some disadvantages compared to invertebrates in their degree of safety from predators: (1) The Varied Tit is less vigilant while handling them since its ability to detect a predator is greater when it is raising its head (Lima et al. 1999); (2) predators might be able to locate the tit on the basis of its loud hammering noise (Székely et al. 1989); and (3) unspoiled acorns are distributed in the outer parts of trees where the vegetation cover was destroyed most severely. We suggest that the Varied Tit gave up foraging on acorns under the decreased vegetation cover, as a trade-off between effi-

cient foraging and safety from predators while foraging on acorns. Furthermore, this shift in the diet could also be attributed to the increased mixed-species flock attendance rate of the Varied Tit, since the benefit of copying other species might be greater when they feed on cryptic invertebrates (Waite & Grubb 1988). The Great Tit, in contrast, did not show any changes in its diet, which might be because its diet consisted of invertebrates that are easier to handle than plant products, and because they are distributed in various parts of the trees.

The changes in the preferred foraging heights after the typhoon might also be due to the predation risk. The reduction of cover was most notable in the upper layer, which the tits avoided after the disturbance. However, the new foraging heights, where the tits appeared after the typhoon, differed between the Varied and Great tits. There are several possible reasons for this difference, such as inter-specific relationships (Nakamura & Shindo 2001) and the distribution of food resources, although we cannot discuss these in detail as we know little about the quality of each foraging substrate, the dominant-subordinate relationship in the mixed-species flocks, or the movement of leading species.

We therefore conclude that the changes in foraging and flocking behavior after the typhoon were mainly due to the increased predation risk caused by reduced vegetation cover.

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SPECIAL FEATURE Interspecific segregation and attraction in forest birds

Foraging mode shifts of four insectivorous bird species under temporally varying resource distribution in a Japanese deciduous forest

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Abstract Temporal changes in the foraging habitat of four forest bird species and the distribution pattern of arthropod populations were investigated. The abundance and distribution of arthropods changed drastically with the season within the forest. Lepidoptera larvae were most abundant in the canopy in the first three weeks after budbreak; their numbers decreased rapidly during mid-June. In contrast, on the forest floor, the larvae were abundant from early to late June. The foraging height of the Narcissus Flycatcher *Ficedula narcissina* changed in parallel with the distribution pattern of Lepidoptera larvae. Three other species, the Great Tit *Parus major*, Marsh Tit *P. palustris*, and Eastern Crowned Warbler *Phylloscopus coronatus*, however, did not change their foraging heights; they continued to forage in the canopy. These differences are probably due to the greater preference of the flycatcher for Lepidoptera larvae compared with the other three species. The three other species switched from feeding on Lepidoptera larvae to spiders or other arthropods in mid June, when the number of Lepidoptera larvae decreased in the canopy. The results of this study suggest that the abundance and distribution of arthropods and differences in foraging tactics among bird species considerably affect avian foraging habitat. The foraging behavior of three species of forest birds revealed species-specific responses to spatio-temporal fluctuations in the distribution of resources.

Key words Forest bird, Foraging tactics, Lepidoptera larvae

Since Lack's (1971) findings of a clear-cut partitioning of foraging substrates in tree crowns among tit species, other studies have confirmed a close relationship between bird foraging habit and resource distribution (Alatalo 1980; Holmes & Schultz 1988). Forest bird species have been shown to co-exist by partitioning their food resources by segregating their foraging habitats (MacArthur 1958; Lack 1971; Schoener 1974). However, studies of forest avian communities have usually been conducted under rather stable circumstances (Wagner 1981; MacNally 1994). The spatio-temporal variation in resource distribution can considerably affect the foraging behaviors of birds, and hence bird communities (Wiens 1989; Maurer 1990).

In reality, the distribution of food resources for in-

sectivorous birds within a forest change drastically with the season (Raupp et al. 1988; Hunter 1991). In temperate deciduous forests, the abundance and distribution of herbivorous insects, in particular Lepidoptera larvae, which are the most preferred prey of insectivorous forest birds (Royama 1969), change dramatically in spring due to strengthening defence traits of tree leaves after budbreak (Feeny 1970; Murakami & Wada 1997). Moreover, most bird species require greater resources for feeding their nestlings and fledglings in this season (Holmes et al. 1979; Burke & Nol 1998). It has also been concluded that food often limits the reproduction and survival of forest birds during their breeding season (Martin 1987; Rodenhouse & Holmes 1992). It is, therefore, expected that temporal changes in foraging behavior among birds in response to the abundance and distribution of arthropods should affect the fitness of individual birds, and hence the structure of the avian community. Although van Noordwijk et al. (1995)

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suggested a relationship between the timing of Great Tit breeding and the availability of Lepidoptera larvae as food for their fledglings, the responses of birds to temporal changes in resource abundance and distribution have been little studied. Further understanding of species-specific responses of birds to temporal changes in resource abundance and distribution in deciduous forests in spring will help to explain the composition of local bird communities (cf. Holmes et al. 1979; Robinson & Holmes 1982; Hino 1994).

Hejl and Verner (1990) suggested that some species of birds living in the same habitat undergo similar changes in foraging behavior and diet as temporal changes affect resource abundance and distribution. In this study, I hypothesized that all forest bird species change their foraging habitat according to the distributional changes in Lepidoptera larvae. To evaluate this hypothesis, I measured the abundance and distribution of arthropods within a forest during spring and early summer and quantified the differences in the foraging behavior of four forest bird species, Great Tit *Parus major*, Marsh Tit *P. palustris*, Narcissus Flycatcher *Ficedula narcissina*, and Eastern Crowned Warbler *Phylloscopus coronatus*, in response to the changes in resource distribution.

STUDY AREA AND METHODS

Field studies were performed in a 9 ha (300×300 m) plot in Tomakomai Experimental Forest (TOEF) of Hokkaido University in northern Japan (42°43'N, 141°36'E; 50–95 m elevation). Oak *Quercus crispula*, maple *Acer mono*, and linden *Tilia japonica* dominate the vegetation of the study plot. A 20-m square grid was set up on the forest floor using color markers. The buds of the deciduous trees opened in mid May. Two resident insectivorous bird species, the Great Tit and the Marsh Tit, began to brood in mid May, and two migrant bird species, Narcissus Flycatcher and Eastern Crowned Warbler, began to brood in late May (cf. Ishigaki & Matsuoka 1972). Fledgling Great Tits and Marsh Tits were observed to leave their nests during late May and early June, and those of Narcissus Flycatcher and Eastern Crowned Warbler, during early and mid June. Secondary nests were built by two pairs of Great Tit in the study area.

Within the study plot, I measured the vertical foliage distribution on 8 July, 1995. The presence or absence of foliage above each of the color markers

(n=256) for bird observation grids was recorded for each of the following height layers: 0–0.5 m, 0.5–1.5 m, 1.5–3 m, 3–5 m, 5–7 m, 7–10 m, 10–15 m, 15–20 m, >20 m). The percentage of foliage present in each layer, P_i , was calculated as $P_i = (p_i/256) \times 100\%$, where p_i is the number of observation points above which foliage is present at the i th height layer. The canopy top was 15 to 25 m high, and saplings and current year seedlings of the dominant tree species grew in the shrub layer (0–1.5 m). The foliage was rather sparse at 1.5–5 m under the dense foliage at 7–15 m.

Sampling of arthropods. To reveal the seasonal changes in arthropod distributions in the canopy trees (canopy) and in the understory vegetation (forest floor), two different sampling methodologies were conducted simultaneously in the forest around the bird observation plot. Arthropods in the canopy were collected using the beating method, and those on the forest floor were collected by sweeping.

One individual of oak was chosen randomly for each sampling period. The oak canopy was sampled weekly from 25 May to 6 July 1995. Climbing to the canopy layer (10–25 m high) using Perry's (1978) method, I beat branches repeatedly, and collected arthropods which dropped onto a tray (80×80 cm) beneath the branches. This was replicated randomly ten times for different parts of an individual tree. For each sample, I selected a single tree that had not previously been sampled.

Arthropods on the forest floor were collected by sweeping every week from 1 June to 13 July. For each sample, a 40 cm diameter insect net was swept continuously for 30 min. within a 400 m² square on the forest floor. The same area was sampled only once during the study period. The arthropods collected were classified into two categories, Lepidoptera larvae and other arthropods, and the number of individuals was counted separately for each category.

Bird foraging ecology. Individuals of the four dominant bird species were identified by color rings, and their foraging behavior was observed for five consecutive days each week during the breeding season from 24 May to 5 July 1995. An observer walked through the study plot on a systematic basis (cf. Kendigh 1944) from 05:00 to 11:00 hr. No more than 10 foraging maneuvers for each individual bird encountered were observed, these included both feeding for nestling or fledglings and foraging for themselves. The feeding of nestlings or fledglings ac-

counted for about 80% of all foraging maneuvers. On average, an individual bird was observed continuously for 3.5 min. during which it averaged 6.2 foraging maneuvers. Whenever the individual bird being observed made a foraging maneuver, the height at which it foraged, the prey type (Lepidoptera larvae or other arthropods), the kind of attack (sallying, gleaning, or pecking, and the substrate were recorded; cf. Holmes et al. 1979). Foraging heights were estimated to the nearest two metres. An individual previously observed on the same day was left out so as to avoid a bias due to a particular individual. The kinds of attacks and substrates were combined into seven different foraging behaviors: 1) Air Sally, 2) Leaf Sally, 3) Leaf Glean, 4) Leaf Pecking, 5) Twig and Trunk Sally, 6) Twig and Trunk Glean, and 7) Twig and Trunk Pecking. The daily mean height of the foraging site was calculated for each individual bird. The percentage of foraging on Lepidoptera larvae (Prey Type) and those of each foraging method were calculated for each day. The daily data were summed for each week of the survey period.

Statistical analyses. A two-way ANOVA (factor=period, arthropod category) was used to reveal seasonal changes in the abundance of the two arthropod categories in the canopy. The weekly changes and inter-specific differences in the foraging height and the proportion of Lepidoptera larvae in bird prey was analyzed by two-way ANOVA (factor=time, bird species). Furthermore, the seasonal and inter-specific difference in foraging behavior was analyzed by a two-way MANOVA (factor=time, species) based on the frequencies of each foraging method. Exact values were \log_{10} transformed and percentage data were arc-sin transformed to standardize variances and improve normality, if necessary to satisfy the assumptions of the ANOVAs. All statistical tests were two-tailed. In all cases, statistical significance was evaluated at $P < 0.05$.

RESULTS

Arthropod distribution. A two-way ANOVA revealed significant effects of both sampling period ($F=12.84$, $df=6$ and 126 , $P < 0.001$) and arthropod category ($F=4.20$, $df=1$ and 126 , $P=0.043$; Fig. 1a). The interaction effect was also significant ($F=4.25$, $df=6$ and 126 , $P=0.002$). The number of Lepidoptera larvae showed a conspicuous peak during late May to mid June. Thereafter, it decreased rapidly and remained at a low level from late June to July. The

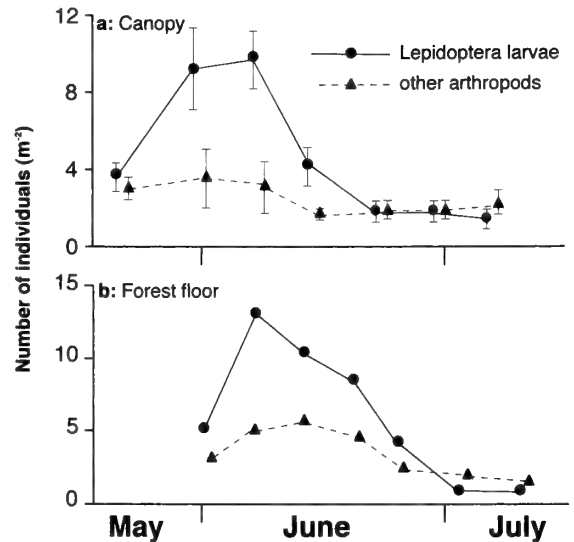


Fig. 1. Seasonal changes in the numbers of arthropods in the canopy (a), and on the forest floor (b). Solid lines indicate Lepidoptera larvae and dotted lines other arthropods. Error bars are standard errors of the means.

number of other arthropods showed a smaller peak than that of the Lepidoptera larvae from late May to early June. The number of Lepidoptera larvae was larger than that of other arthropods from late May to mid June.

On the forest floor, the number of Lepidoptera larvae peaked in early June, then gradually decreased and reached a low level in late June (Fig. 1b). The number of other arthropods showed a rather small peak in mid June.

Bird foraging habitat. In the study plot, 11 individual Great Tits, 16 Marsh Tits, 21 Narcissus Flycatchers, and 19 Eastern Crowned Warblers were recorded during the study period. Foraging height varied significantly seasonally ($F=6.47$, $df=5$ and 15 , $P < 0.001$; Fig. 2b) and among bird species ($F=137.0$, $df=3$ and 15 , $P < 0.001$) with significant interaction ($F=7.95$, $df=18$ and 15 , $P < 0.001$). Great Tits, Marsh Tits, and warblers continued to forage in the canopy throughout the study period, whereas flycatchers changed their foraging height. Flycatchers foraged in the canopy from late May to mid June, then on the forest floor from mid June to late June, and again in the canopy from late June to early July.

Prey types were identified in 68% of the 3,857 foraging maneuvers observed. The prey type varied significantly seasonally ($F=64.96$, $df=5$ and 96 , $P < 0.001$; Fig. 3) and among bird species ($F=5.647$, $df=3$ and 96 , $P=0.0013$) with significant interaction

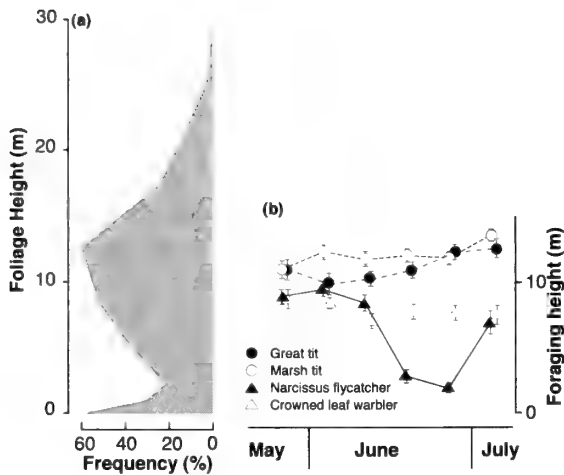


Fig. 2. Vertical foliage distribution in the study plot (a), and seasonal changes in the foraging height of four-bird species (b). Error bars are standard errors of the means.

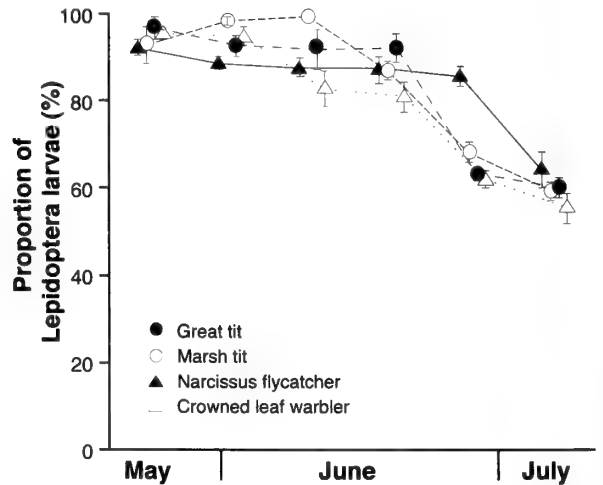


Fig. 3. Seasonal changes in the proportion of Lepidoptera larvae preyed on by four bird species. Error bars are standard errors of the means.

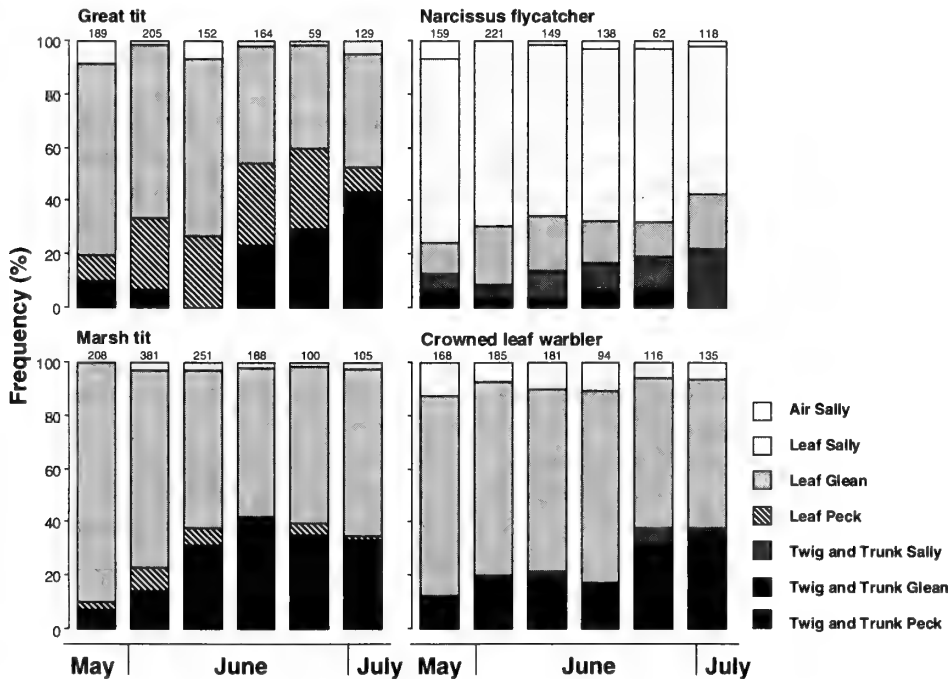


Fig. 4. Seasonal changes in relative frequencies of each of the foraging behaviors employed by four bird species. The letters on the top of each bar were the numbers of observation for each bird species in each period.

($F=4.371$, $df=15$ and 96 , $P<0.001$). From late May to mid June, all four bird species foraged mostly on Lepidoptera larvae. In late June, the flycatchers continued to forage on Lepidoptera larvae, whereas the three other species reduced their utilization ratio of Lepidoptera larvae. Then in July, all four species utilized the Lepidoptera larvae at a ratio of about 60%.

The MANOVA analysis revealed that foraging behavior differed both among bird species (Hotelling-

Lawley Trace: bird species, value=12.77, $F=53.94$, $df=21$, $P<0.001$) and across the seasonal period (value=1.669, $F=2.176$, $df=35$, $P<0.001$; Fig. 4) with significant interaction (value=1.667, $F=1.404$, $df=105$, $P=0.008$). Flycatchers mostly foraged by sallying from leaves throughout the study period (more than 60% of all foraging maneuvers) and rarely utilized twigs and trunks ($<15\%$). The three other species frequently foraged by gleaning from

leaves. Great Tit also foraged by pecking on leaf rolling caterpillars, and Marsh Tit by pecking on twigs and trunks. From late June to July, these three species came to forage more frequently on twigs and trunks (about 40%) than in the previous period (about 20%).

DISCUSSION

Lepidoptera larvae were abundant in the oak canopy from late May to mid June, and then rapidly decreased. The spring foliage is known to open a "window" of high quality leaves for herbivorous insects but only for a short duration, which causes changes in the abundance and distribution of herbivorous insects (Feeny 1970; Kraft & Denno 1982; Murakami & Wada 1997). In the present study, Lepidoptera larvae disappeared rapidly from the canopy after early June, but became abundant on the forest floor during early to mid June. Many Lepidoptera larvae are known to migrate from the canopy to the floor for pupation or to seek alternative food resources when canopy leaves strengthen their defence traits during this season (Murakami & Wada 1997). In contrast, other arthropods, most of which are not herbivores (e.g. spiders and dipterans), did not make such a drastic distributional change.

The present study showed that Narcissus Flycatchers shifted their foraging height nearly in parallel with the change in distribution of Lepidoptera larvae. They foraged in the canopy from late May to early June, then on the forest floor from mid to late June, confirming the results of my previous study conducted in 1994 (Murakami 1998). Such a shift was nearly synchronous with the decline in Lepidoptera larvae biomass in the canopy, but a little later than the peak of larval abundance on the forest floor, thus implying that the foraging habitat shift was due to the decline of Lepidoptera larvae in the canopy rather than the increase of the larvae on the floor. The three other bird species, however, continued foraging in the canopy even after this critical moment. During this study, Narcissus Flycatchers foraged intensively on Lepidoptera larvae, shifting their foraging site from the canopy to the forest floor in late June, when the abundance of larvae in the canopy decreased. In contrast, the three other bird species continued to forage in the canopy, but shifted their foraging substrate there from leaves to twigs or trunks, and shifted their main prey from Lepidoptera larvae to other arthropods. Thus, the Narcissus Flycatcher and the three

other bird species coped differently with the abrupt change in the abundance of Lepidoptera larvae as the most important food resource in the canopy.

The different responses among these four species should correspond to their species-specific foraging tactics. Rosenberg (1993) suggested that the foraging tactics utilized by birds considerably affect the accessibility of prey organisms on different substrates. Moreover, it has been suggested that differences in foraging methods affect a bird's prey-type selection and that gleaners can obtain smaller prey than salliers (Holmes & Recher 1986). In this study, the flycatcher mainly performed sallies, whereas the other species frequently fed by gleaning or pecking. The flycatcher probably changed its foraging habitat after having difficulty in finding alternative food resources in the canopy during mid and late June when Lepidoptera larvae, which are far larger than other available arthropods within the forest (Murakami unpubl. data), disappeared from the canopy. The three other species, however, did not change their foraging layer in this season. Instead, they began to frequently utilize other arthropods as alternative resources. In early July, the flycatcher resumed foraging in the canopy. When the density of Lepidoptera larvae was low both in the canopy and on the forest floor, the flycatcher, due to its innate foraging behavior (Wiens 1984), probably foraged more efficiently in the canopy than on the floor. Because the fledglings of all four bird species had already left their nests by this season, breeding phenology should have little or not effect on the differences observed in foraging site selection.

The presence of species that prey on birds can also affect the foraging site selection of birds (Székely et al. 1989). A location that is covered by foliage may be safer than an exposed one (Ekman 1987). In the study plot, Japanese Lesser Sparrowhawk *Accipiter gularis* was observed five times during the study period (Murakami pers. obs.). The ground layer (0–5 m) of this forest was not densely covered by foliage (Fig. 2), which indicates that birds on the ground may be at greater risk of predation by birds. Therefore, it is expected that Narcissus Flycatchers selected a rather risky habitat in order to be able to forage on Lepidoptera larvae. Interspecific competition among bird species may also affect foraging habitat selection (Alatalo et al. 1987). Although there was no direct evidence for interspecific competition in this study, the differences in foraging heights among the four bird species (Fig. 2) may indicate that interspecific competition was operating.

Given that previous studies have shown that seasonal shifts in foraging mode coincide among different bird species in the same habitat due to the change in prey availability (Alatalo 1980; Rotenberry & Wiens 1980; Hejl & Verner 1990), I hypothesized that all four bird species tracked the distributional change in Lepidoptera larvae. My results, however, indicated that each bird species responds differently to the changes in resource distribution according to their foraging tactics, which may be limited by their species-specific morphological structure as shown by Moreno and Carrascal (1993). Further investigation of the relations between such versatile foraging behaviors of birds and fluctuation of resource abundance and distribution will provide a deeper insight into the mechanisms of species co-existence in bird communities (cf. Smith & Rotenberry 1990).

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The effects of arthropod abundance and size on the nestling diet of two *Parus* species

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Abstract Feeding habits of *Parus major* and *P. varius* inhabiting coniferous plantations of *Cryptomeria japonica* and *Larix kaempferi*, each containing a small area of deciduous broad-leaved trees, were analyzed in relation to the abundance and size distribution of arthropods. In a *C. japonica*-dominated (CJ) area, *C. japonica* trees were mainly used by *P. major* only, while deciduous broad-leaved trees were used by both *Parus* species. In a *L. kaempferi*-dominated (LK) area, both *Parus* species used *L. kaempferi* trees and deciduous broad-leaved trees. The composition of nestling diets differed between *Parus* species. For prey size, the difference in the breadth was smaller and the overlap was larger between areas than between species. These results suggest that each *Parus* species preferred a specific size class of prey. That is, the single-prey loader *P. major* preferred large prey, whereas the multiple-prey loader *P. varius* preferred small prey. The abundance and size distribution of arthropods greatly differed among foraging microhabitats. Both *Parus* species selectively used foraging microhabitats according to their prey-size preference.

Key words Diet selection, Foraging microhabitat, Nestling diet, *Parus major*, *Parus varius*, Size preference

Forest-dwelling insectivorous birds, including Paridae, depend on arthropods for food, especially during the breeding season. The structure, biomass and dynamics of arboreal arthropod communities may vary depending on the tree species composition and structural features of forests (e.g. Stork et al. 1997), thus the characteristics and availability of arthropods as a food resource for insectivorous birds may differ among different forest types. In general, *Parus* species depend on caterpillars, mostly lepidopteran and hymenopteran larvae, for primary food resources (Perrins 1979), but their food composition differs among forest types (Gibb & Betts 1963; van Balen 1973). Although many studies have focused on the effects of differences in the availability of caterpillars on the feeding habits or breeding ecology of *Parus* species (e.g. van Balen 1973; Yui 1988; Perrins 1991; van Noordwijk et al. 1995; Seki & Takano 1998), little attention has been paid to other arthropods, or to the whole arthropod community, as potential food resources.

According to the optimal-foraging theory, predators choose their diet to maximize their net rate of energy intake (cf. Krebs & Kacelnik 1991). Thus, the characteristics of arthropods, such as abundance, biomass and other specific features associated with their susceptibility to capture, are relevant to the profitability of each prey item and thus to the foraging decision by birds (Royama 1970; Hespenheide 1975). Also, it has been known for some time that birds differ interspecifically in their prey-size preferences, presumably associated with their morphological traits (e.g. Betts 1955; Gibb & Betts 1963; Diamond 1973; Eguchi 1979; Quinney & Ankney 1985; Török 1986; Díaz 1994).

In this paper, we describe the feeding habits of *Parus major* and *P. varius* in two coniferous plantations of the evergreen *Cryptomeria japonica* D. Don and the deciduous *Larix kaempferi* Carrier. Marked differences in the abundance, biomass, and composition of the arthropod community has previously been revealed between these two plantations (Hijii et al. 2001; Mizutani & Hijii 2001).

We demonstrate the effects of the abundance and size distribution of arthropods on microhabitat selec-

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tion by *Parus* species through their prey-size preference for their nestlings.

MATERIALS AND METHODS

1) Study site

The study was carried out in the Nagoya University Forest at Inabu, Aichi Prefecture, central Japan (980–1230 m a.s.l.; 35°11'N, 137°33'E). The annual air temperature averaged 8.3°C and the mean annual precipitation was 2250 mm (1981–1998). About 90% of the area of this experimental forest is dominated by plantations of *C. japonica*, *L. kaempferi* and *Chamaecyparis obtusa* Sieb. et Zucc. Small stands of deciduous broad-leaved trees such as *Quercus crispula*, *Carpinus tschonoskii*, *Prunus grayana* and *Acer sieboldianum* occur patchily, for the most part along ridges and streams. The height of dominant trees was 20–25 m and the age of the plantations was 21–40 years. The canopies of the plantations were closed; their understories were not dense and were heterogeneous, consisting mainly of *Lindera praecox* and *L. triloba*. For the purposes of this study, understory was defined as the ground flora rising no more than two metres above the ground.

Two adjoining study areas were established in the experimental forest: a *C. japonica*-dominated (CJ) area and a *L. kaempferi*-dominated (LK) area (Fig. 1). More than 50% of each area was covered with a plantation of each dominant conifer, while about 10% of each area consisted of deciduous broad-leaved trees. The remainder of each area consisted mainly of *Chamaecyparis obtusa* plantations and bare areas, both of which were rarely used by either *Parus* species. Censuses were conducted during the nestling period of early broods of the two *Parus* species in 1999.

2) Foraging microhabitat

From 23 May to 9 June 1999, the microhabitat use of foraging *Parus* species was surveyed using a line-census method. In each study area, two transects, each 50-m wide and 3.8-km long, covering 40% of the area, were surveyed six times. Whenever a bird was observed to forage on a prey item, its height above the ground, and the plant species from which it foraged, were recorded. Foraging microhabitat selection for tree layers was analyzed using the selectivity index defined as the ratio of percentage microhabitat use to percentage cover area for each tree species (Manly et al. 1993). The selectivity index is 0 when

the resource is not used at all, 1 when the resource is used as expected by chance, and larger than 1 when the resource is used selectively.

3) Nestling diet

From 14 May to 16 June 1999, nestling diet was recorded with an 8-mm video camera at six clutches of *P. major* (3 at CJ area and 3 at LK area) and five clutches of *P. varius* (3 at CJ area and 2 at LK area) in nest boxes. For each observation, two trials, each of six hours, were made in the first half (5–9 days of age) and the latter half (11–15 days of age) of the nestling period. We converted the recorded video movie into a computer file in non-compressed video format, then extracted several still images for each nest-visit. From the still images, prey items (at the order level or as "caterpillars"), and prey-size (body length) were recorded. Totals of 1181 feeding records were obtained on video for *P. major* and 406 for *P. varius*. Among them, clear pictures suitable for prey identification and for prey-size determination amounted to 1124 for *P. major* and 330 for *P. varius*. Dry weights (W, mg) of prey items were estimated from body lengths (L, mm) and regression equations made based on field samples (caterpillars and orthopteran insects) collected randomly in the study site

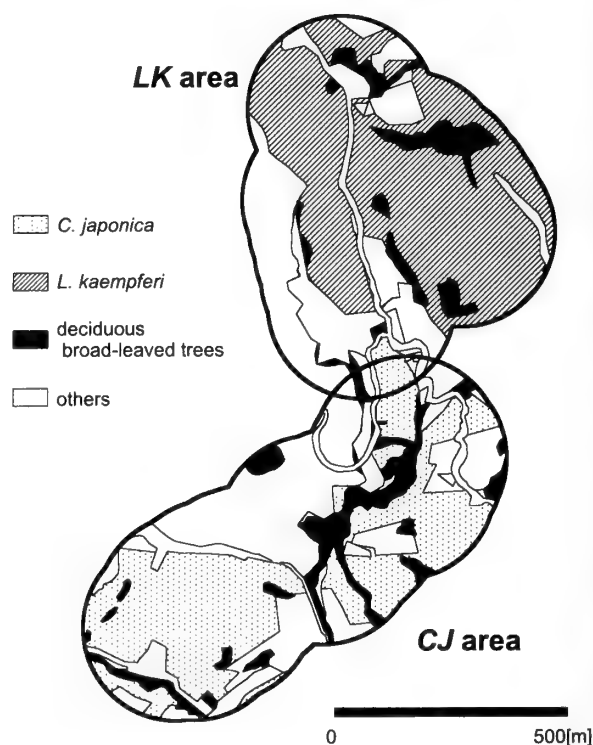


Fig. 1. The vegetation of the two study areas.

during the nestling period of early broods of two *Parus* species or from the literature.

For caterpillars the dry weight estimate was:

$$W=0.0011L^{3.60} \quad (n=103, r^2=0.91, P<0.001) \quad (1)$$

for orthopteran insects it was

$$W=0.0120L^{2.36} \quad (n=88, r^2=0.94, P<0.001) \quad (2)$$

and for other arthropods

$$W=0.0305L^{2.62} \quad (r^2=0.94: \text{Rogers et al. 1976}). \quad (3)$$

Prey size was defined as the dry mass (estimated as above) and classified according to size classes between 10^{-1} and $10^{2.5}$ mg dry weight (d.wt) at intervals of the power index 0.25. The breadth of the size-class distribution for prey items was evaluated using the Shannon-Wiener formula (Shannon & Weaver 1949),

$$H' = - \sum_j p_j \log p_j \quad (4)$$

where p_j is the proportion of prey individuals belonging to size class j . The degree of overlap between size-class distributions was evaluated using the multiplicative measures of niche overlap (Pianka 1973),

$$\alpha_{hi} = \frac{\sum_j p_{hj} p_{ij}}{\sqrt{\sum_j (p_{hj})^2 \sum_j (p_{ij})^2}} \quad (5)$$

where p_{hj} and p_{ij} are the proportions of prey individuals of the j th size class used by the h th and the i th species, respectively. The index α varies from 0, when size-class distributions are completely distinct, to 1, when they fully overlap.

4) Arthropod sampling

Arthropod sampling was conducted twice, on 18 May and 10 June 1999. Arthropods were collected from four foraging microhabitats: tree layers of *C. japonica*, *L. kaempferi* and deciduous broad-leaved stands using the branch clipping method, and from the understory using the beating method. Details of the protocol for the branch clipping method are described by Hijii et al. (2001). Arthropod sampling from *C. japonica* and deciduous broad-leaved stands was made in the *CJ* area, and that from a *L. kaempferi* stand in the *LK* area. Since the two study areas were contiguous, and because the vegetation in the deciduous broad-leaved stands in both areas were similar, we assumed that the characteristics of the

arthropods on the foliage of deciduous broad-leaved stands in the *CJ* area could be substituted for those in the *LK* area. On each of the two arthropod sampling dates, five branch-clipping samples were taken from *C. japonica*, five from *L. kaempferi*, and three from deciduous broad-leaved trees. Each sample consisted of two or three 60–80 cm long branches (leaves and associated twigs and branches) collected randomly from three trees from the coniferous stands, and two 30–40 cm long branches from 10 trees from the deciduous broad-leaved stands. Arthropod specimens from the understory were collected from each of the above three stands during one trial involving beating for 10 minutes in a 2×30 m quadrat. The data from the understories of the three stands were combined for the analysis. All branch-clipping and beating samples were treated immediately with an insecticide, scrutinized to collect all the arthropods (>1 mm) and then stored in 70% ethanol within 72 hours. These arthropods were identified, their body lengths were measured with a digital calliper or a micrometer under a binocular microscope, and then their individual dry weights were estimated by using equations (1)–(3) above. The density of arthropods was evaluated from the number or biomass per unit foliar mass for branch-clipping samples, while that for beating samples was evaluated in terms of the number or biomass per trial.

RESULTS

1) Foraging microhabitat

Significant differences in the use of five microhabitats were found between *Parus* species in the *CJ* area (extended Fisher's exact probability test, $\chi^2=32.75$, $df=4$, $P<0.001$), but not in the *LK* area ($\chi^2=1.92$, $df=4$, $P=0.75$) (see Table 1). The proportion of understory use did not differ significantly between *Parus* species nor between areas (Fisher's exact probability test, $P>0.05$ for each combination).

With respect to canopy layers, both *Parus* species used the foliage of deciduous broad-leaved trees more frequently than expected by chance in both areas (Table 1). *P. varius*'s preference for deciduous broad-leaved trees was much higher than that of *P. major* in the *CJ* area, but slightly lower in the *LK* area. Among the coniferous microhabitats, *P. major* used *C. japonica* in the *CJ* area and *L. kaempferi* in the *LK* area almost randomly, whereas *P. varius* scarcely used *C. japonica* in the *CJ* area but used *L. kaempferi* in the *LK* area almost at random.

Table 1. Foraging frequency and microhabitat selection in canopy layers by *P. major* and *P. varius* in each study area. The values of coverage for each transect and of foraging frequency are shown as percentages in parentheses. The selection ratio is defined as the ratio of the proportion of foraging frequency (except in the understory), to the proportion of microhabitat coverage. The χ^2 value was calculated after Manly et al. (1993). Levels of statistical significance were obtained after applying the Bonferroni correction. ns, $P>0.05$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Foraging microhabitat	Coverage of transect [ha]	Foraging frequency	Selection ratio	χ^2 -value
<i>P. major</i>				
<i>CJ</i> area				
<i>C. japonica</i>	8.41 (54.6)	17 (53.1)	1.15	0.76 ^{ns}
<i>L. kaempferi</i>	0 (0.0)	1 (3.1)	—	—
deciduous broad-leaved trees	2.15 (14.0)	6 (18.8)	1.59	1.53 ^{ns}
others	4.83 (31.4)	3 (9.4)	0.35	5.15**
understory	—	5 (15.6)	—	—
<i>LK</i> area				
<i>C. japonica</i>	0.08 (0.5)	0 (0.0)	—	—
<i>L. kaempferi</i>	9.46 (63.3)	23 (52.3)	0.96	0.14 ^{ns}
deciduous broad-leaved trees	2.11 (14.1)	11 (25.0)	2.05	8.00**
others	3.30 (22.1)	4 (9.1)	0.48	3.42*
understory	—	6 (13.6)	—	—
<i>P. varius</i>				
<i>CJ</i> area				
<i>C. japonica</i>	8.41 (54.6)	11 (12.6)	0.25	58.68***
<i>L. kaempferi</i>	0 (0.0)	0 (0.0)	—	—
deciduous broad-leaved trees	2.15 (14.0)	64 (73.6)	5.72	315.43***
others	4.83 (31.4)	5 (5.7)	0.20	25.53***
understory	—	7 (8.0)	—	—
<i>LK</i> area				
<i>C. japonica</i>	0.08 (0.5)	1 (0.9)	—	—
<i>L. kaempferi</i>	9.46 (63.3)	62 (57.4)	0.98	0.08 ^{ns}
deciduous broad-leaved trees	2.11 (14.1)	26 (24.1)	1.84	12.62***
others	3.30 (22.1)	11 (10.2)	0.50	7.72**
understory	—	8 (7.4)	—	—

2) Composition and size distribution of prey items

In both study areas, *P. major* was always a single-prey loader, whereas *P. varius* carried multiple prey items at a time to its young. The number of prey items carried per visit by *P. varius* differed significantly between areas (Mann-Whitney U-test, $U = 9.96 \times 10^3$, $P = 0.02$) (Fig. 2).

The main nestling diet of both *Parus* species consisted of caterpillars and orthopteran insects (Fig. 3). The nestling diet of *P. varius* was dominated by caterpillars, which accounted for 76–94% (in number) of the whole nestling diet for each brood. In contrast, the main nestling diet of *P. major* comprised not only caterpillars (17–51%), but also orthopteran insects (42–75%; mainly Anoplophidae), and spiders (ca. 4%). The composition of *P. major*'s diet varied greatly between areas: the proportion of caterpillars in the diet was lower in number in the *CJ* area than in

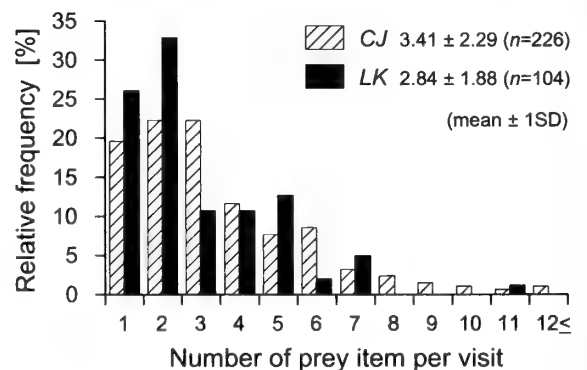


Fig. 2. Frequency distribution of the number of prey items per visit of *P. varius*.

the *LK* area. The composition of the nestling diet differed significantly between *Parus* species (G-test with Bonferroni correction, $G = 634.7$, $P < 0.001$ for

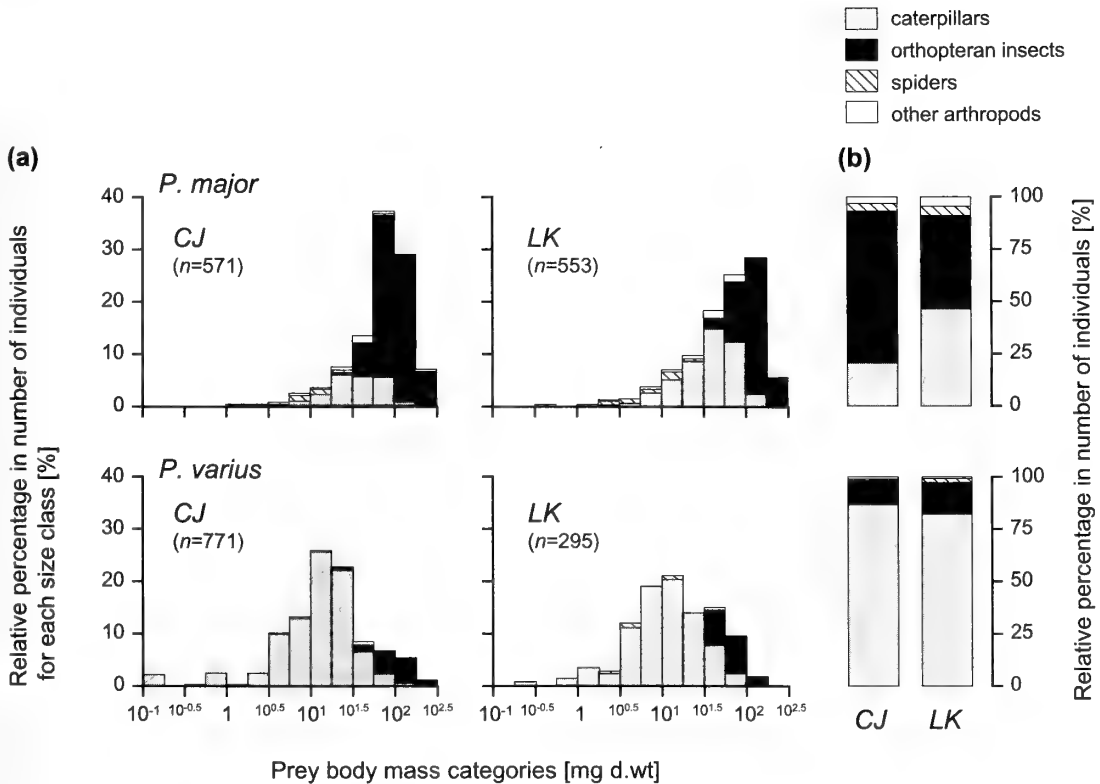


Fig. 3. Size distribution (a) and relative composition (b) of prey items used by *P. major* (upper) and *P. varius* (lower).

Table 2. Mean body mass (mean \pm 1 SD; mg dry wt) for all prey items and the major prey categories taken by *Parus major* and *P. varius* (sample sizes in parentheses). Levels of significance of differences in mean body mass, based on the Mann-Whitney U-test, are indicated (ns, $P > 0.05$; *, $P < 0.05$; ***, $P < 0.001$).

	Caterpillar	Orthoptera	All prey items
<i>P. major</i>			
CJ area	43.0 \pm 27.8	108.0 \pm 44.3	89.3 \pm 51.0
×	(119)	(414)	(571)
LK area	45.8 \pm 30.5	125.3 \pm 48.2	79.8 \pm 56.9
	(257)	(247)	(553)
<i>P. varius</i>			
CJ area	17.3 \pm 16.3	104.1 \pm 47.9	27.6 \pm 35.9
×	(671)	(91)	(771)
LK area	15.9 \pm 16.5	73.5 \pm 28.5	24.7 \pm 28.0
	(243)	(45)	(295)
<i>P. major</i> × <i>P. varius</i>			
CJ area	***	ns	***
LK area	***	***	***

CJ; $G = 109.2$, $P < 0.001$ for LK) and between areas only for *P. major* (G-test with Bonferroni correction, $G = 95.3$, $P < 0.001$ for *P. major*; $G = 4.25$, $P = 0.24$ for *P. varius*) (Fig. 3).

The minimum body mass of the prey items used by

Parus species was 0.1 mg d.wt (Fig. 3). *P. major* chose larger prey items than *P. varius* for all prey items (Table 2). The mean body mass of all prey items used by *P. major* differed significantly between areas (Mann-Whitney U-test, $U = 1.37 \times 10^5$, $P <$

0.001). Prey items from 10^1 to $10^{2.25}$ mg d.wt accounted for ca. 90% of the nestling diet of *P. major*. The mean body mass of all prey items used by *P. varius* was smaller than that used by *P. major*, and did not differ between areas (U-test, $U=1.07 \times 10^5$, $P=0.12$). About 90% of the nestling diet of *P. varius* consisted of prey items ranging in dry weight from $10^{0.5}$ to 10^2 mg. The caterpillars taken by *P. major* did not differ in size between areas (U-test, $U=1.45 \times 10^4$, $P=0.42$), whereas those taken by *P. varius* did differ between areas (U-test, $U=7.24 \times 10^4$, $P<0.01$).

P. varius took prey of a broader range of size classes, for all prey items, than *P. major* (Table 3). The difference in the breadth of prey size was smaller between areas than between species. The overlap in the prey-body-size distribution was larger between areas than between *Parus* species (Table 4). The same results were found for caterpillars, but not for Orthoptera.

The smaller difference in the breadth, and the larger overlap for prey size, between areas than between species, suggests that both *P. major* and *P. varius* had specific prey size class preferences.

3) Composition and size distribution of arthropods in foraging microhabitats

The number of individuals of arthropods larger than 0.1 mg d.wt accounted for 94% of all individu-

Table 3. Breadth of the size class distribution for all prey items and the major prey categories (H').

	Caterpillar	Orthoptera	All prey items
<i>P. major</i>			
CJ area	1.58	1.19	1.62
LK area	1.67	1.08	1.83
<i>P. varius</i>			
CJ area	1.86	1.31	2.05
LK area	1.92	0.96	2.05

Table 4. Overlap of the size-class distribution for all prey items and the major prey categories (α).

	Caterpillar	Orthoptera	All prey items
Overlap between areas (CJ×LK)			
<i>P. major</i>	0.97	0.91	0.96
<i>P. varius</i>	0.95	0.71	0.93
Overlap between bird species (<i>P. major</i> × <i>P. varius</i>)			
CJ area	0.64	0.99	0.40
LK area	0.56	0.49	0.54

als. The number of individuals and biomass of all arthropods was highest in deciduous broad-leaved trees and lowest in *C. japonica* (Table 5).

The mean body mass of major prey categories (caterpillars, orthopteran insects and spiders) also differed among foraging microhabitats (Table 6). The caterpillars on *L. kaempferi* foliage were significantly smaller than those on deciduous broad-leaved tree foliage or in the understory. The spiders obtained from *C. japonica* foliage were significantly smaller than those in the three other foraging microhabitats were. The mean body mass for all major prey categories was largest in *C. japonica* foliage, where a large orthopteran insect occurred, whereas mean body mass was smallest in *L. kaempferi* foliage, which was dominated by small caterpillars and spiders. These major prey types contributed relatively large proportions of the whole arthropod fauna: 28.1% (understory)—42.7% (*C. japonica*) in terms of individuals, and 15.8% (*C. japonica*)—38.2% (deciduous broad-leaved trees) in terms of biomass (Fig. 4).

The composition and size distribution of arthropods differed between foraging microhabitats (Fig. 4). The size class of caterpillars most frequently observed in *L. kaempferi* ($10^{-0.5}$ – $10^{0.25}$ mg d.wt) was smaller than that found in deciduous broad-leaved trees ($10^{0.5}$ – $10^{1.25}$ mg d.wt). In the understory, caterpillars of various sizes ($10^{-0.75}$ – $10^{2.25}$ mg d.wt) occurred. Orthopteran insects contributed only 1.4% of the whole arthropod fauna in terms of numbers of individuals, but contributed 13% of the biomass in *C. japonica* owing to the occurrence of one large indi-

Table 5. Numbers of individuals and biomass of arthropods (>0.1 mg dry wt) taken by *Parus major* and *P. varius* in each foraging microhabitat (mean±1 SD). The different letters following values in canopy samples indicate significant differences between mean values according to the Steel-Dwass test ($P<0.05$).

	Number of individuals ¹	Biomass ²
Canopy		
<i>C. japonica</i>	34.6±11.3 ^a	511.4±481.8 ^a
<i>L. kaempferi</i>	429.1±142.2 ^b	2207.0±1758.5 ^b
deciduous broad-leaved trees	1626.0±1277.0 ^c	7933.4±7046.8 ^b
Understory	212.8±57.5	875.4±173.2

¹ Number of individuals and ² biomass (mg dry wt) per unit foliar mass (kg^{-1} dry wt) for the canopy or per trial for the understory

Table 6. Mean body masses (mean \pm 1 SD; mg dry wt) of prey in each foraging microhabitat (sample sizes in parentheses). The different letters following values indicate significant differences in the mean body mass between foraging microhabitats according to the Steel-Dwass test ($P < 0.05$).

	Caterpillar	Orthoptera ¹	Spider	All major prey categories
Canopy				
<i>C. japonica</i>	5.0 \pm 7.4 (3) ^l	139.9 (2)	0.7 \pm 1.3 (56) ^a	5.5 \pm 35.3 (61) ^a
<i>L. kaempferi</i>	2.7 \pm 3.8 (98) ^a		0.9 \pm 1.0 (56) ^b	2.0 \pm 3.2 (154) ^b
deciduous broad-leaved trees	6.8 \pm 6.2 (84) ^b	2.2 \pm 1.1 (5)	1.7 \pm 3.5 (53) ^b	4.7 \pm 5.8 (142) ^c
Understory	8.4 \pm 15.1 (102) ^b	16.7 \pm 23.0 (11)	1.4 \pm 2.1 (246) ^b	3.8 \pm 9.9 (359) ^b

¹ No statistical analysis was performed because of the small sample size.

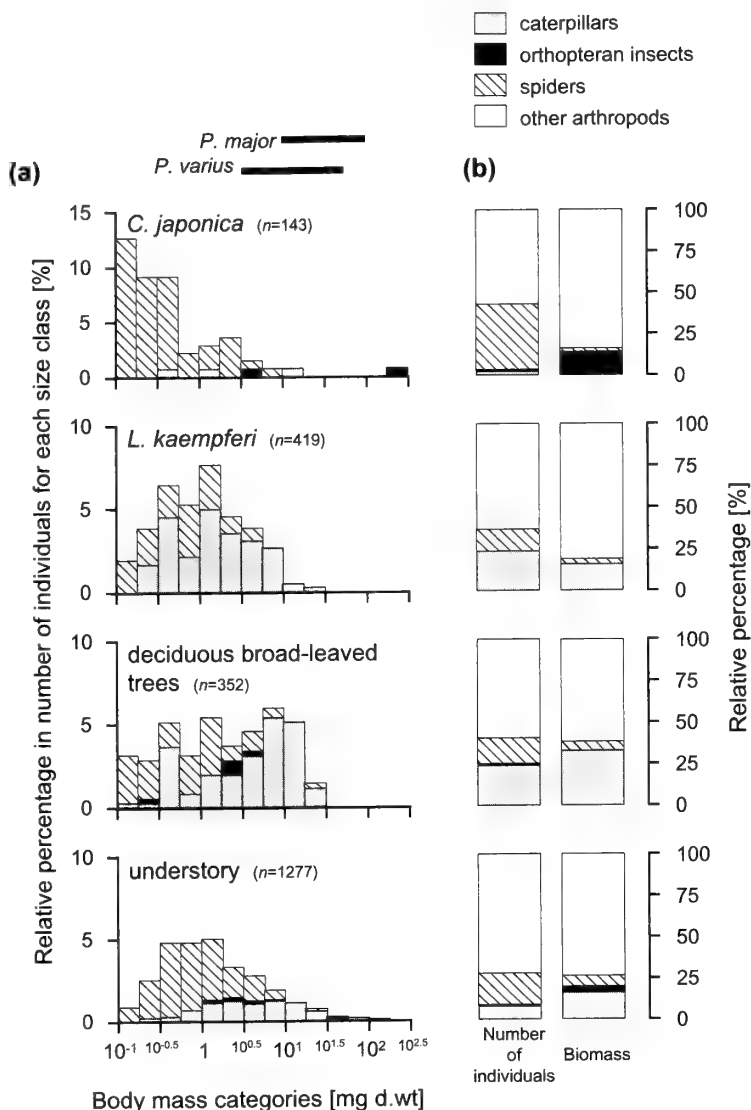


Fig. 4. Size distribution (a) and relative composition in number of individuals and biomass (b) of arthropods collected from each foraging microhabitat. Only arthropods larger than the minimum size of prey items are shown. The horizontal bar above (a) shows the size range containing 90% of caterpillars preyed on by *P. major* and *P. varius*.

vidual (276 mg d.wt). Spider was the most dominant group in number of individuals in all microhabitats, but most of them were less than $10^{0.25}$ mg d.wt.

DISCUSSION

1) Prey size as a contributory factor of nestling-diet selection in two *Parus* species

In this study, two *Parus* species selectively chose prey items of a particular size range specific to each species. The differences in the mean body mass of prey used by each *Parus* species in two study areas were markedly smaller than those between *Parus* species (Table 2). The inter-area differences in the breadth of prey size used by each *Parus* species was small (Table 3) and the inter-area overlap was large (Table 4) in spite of large differences in the body-size distribution (Fig. 4) and other characteristics (Tables 5 and 6) of arthropods between areas. It appears from these results that prey size is more important than prey species for diet selection by these *Parus* species.

The difference in prey size in the diet between sympatric *Parus* species (Table 2) may be due to food-resource partitioning for a relaxation of inter-specific competition. Several authors have reported that preferred prey size differs among *Parus* species (Betts 1955; Gibb & Betts 1963; Eguchi 1985). Sympatric *Parus* species tend to vertically segregate their foraging microhabitats during the non-breeding season (Perrins 1979), and it is also reported that vertical partitioning between *P. major* and *P. varius* did not occur during the breeding season (Nakamura 1970). As reported in Nakamura (1970), the vertical partitioning between those *Parus* species was not found in our study. Because both species preferred deciduous broad-leaved trees, there may have been local competition for foraging microhabitats between them. Nevertheless, they may have been able to avoid competitive interactions by taking different-sized prey.

Food requirements by birds are strongly correlated with their body mass (Nagy 1987). Since the body mass of the two *Parus* species is almost the same (16.5 g fresh weight (f.wt) for *P. major* and 17.0 g f.wt for *P. varius*; Yui 1988), both *Parus* species should have similar feeding efficiencies. The inter-specific difference in prey-size preference could be explained by the fact that whereas *P. major* is always a single-prey loader, *P. varius* is a multiple-prey loader (Fig. 2). *P. varius* may compensate for a decrease in its feeding efficiency by carrying many small prey items at a time.

2) Matching of foraging microhabitat use by *Parus* species with the characteristics of the arthropod community

The characteristics of arthropods as potential prey, such as abundance, biomass (Table 5) and the composition and size distribution of individuals (Table 6, Fig. 4), greatly differed among foraging microhabitats. One of the strategies used by *Parus* species to adapt to mosaic environments with various vegetation types and varying food availability, is selective use of foraging microhabitats with food resources sufficient for reproduction (cf. Dias & Blondel 1996).

Considerable numbers of caterpillars occurred in each foraging microhabitat except in the foliage of *C. japonica*, but their body-size distribution differed among microhabitats (Fig. 4). Orthopteran insects were found in each microhabitat except the foliage of *L. kaempferi* (Fig. 4). In number, their contribution to the whole arthropod fauna was very small, but their contribution to biomass was large because a few large individuals occurred. In this study, the sample size for the branch clipping method may have been insufficient to evaluate the exact abundance and size distribution of orthopteran insects on trees, because of low efficiency of sampling. Our results were similar, nevertheless, to those based on chemical-knockdown samples, which showed that the proportion of orthopteran insects was less than 1% in number, but 16% in biomass (average for the data of June and August; Hijii 1989). Because small orthopteran insects were found both in the foliage of deciduous broad-leaved trees and in the understory, larger individuals may also inhabit both microhabitats. Previously, chemical-knockdown sampling had failed to find orthopteran insects in the foliage of *L. kaempferi* (Terakawa unpubl. data), a fact confirmed by our results. Although spiders have been reported as a secondary major food resource of *Parus* species in many habitats (e.g. Gibb & Betts 1963; Won et al. 1965; Minot 1981; Eguchi 1985; Arakida 1995), they were not a preferred nestling food in our study (Fig. 3). This is probably because small individuals constituted a large proportion of the spiders in number in this study site.

There were significant differences in the use of foraging microhabitats between *Parus* species in the *CJ* area, but not in the *LK* area (Table 1). Both *Parus* species selectively used the foliage of deciduous broad-leaved trees as a foraging microhabitat in both areas. In deciduous broad-leaved trees, various-sized caterpillars available to both *P. varius* ($10^{0.5}$ – $10^{1.75}$)

and *P. major* (10^1 – 10^2) contributed large proportions to the arthropod fauna (Fig. 4). Thus, the foliage of deciduous broad-leaved trees would have been important for both *Parus* species in providing stable food resources. Moreover, there may be more advantageous to *P. varius* capable of using smaller caterpillars, because smaller prey items were abundant, which may enhance the food availability to *P. varius* in this foraging microhabitat (Fig. 4). Thus, *P. varius* could use caterpillars as its main food category (Fig. 3) in both areas.

The foliage of *C. japonica* was mainly used by *P. major*, but only scarcely used by *P. varius* (Table 1). Although the availability of caterpillars was very low, there were large orthopteran insects in the foliage of *C. japonica* (Fig. 4). For *P. major*, which tended to prefer large prey items (Table 2, Fig. 3), orthopteran insects on *C. japonica* trees can be a suitable food resource, even if their abundance is low (Table 1).

In the LK area, both *Parus* species randomly used the foliage of *L. kaempferi*, the preferences for which were lower than for deciduous broad-leaved trees (Table 1). The contribution of individual caterpillars to the overall arthropod fauna was almost the same, but the body-size distribution differed between these microhabitats. The profitability for *P. major* may be lower in *L. kaempferi*, because the proportion of small caterpillars was relatively high. Moreover, both species may not prefer coniferous *L. kaempferi* as much as deciduous broad-leaved trees owing to their morphological adaptations (Nakamura 1978).

In both areas, both *Parus* species also foraged from the understory (about 10% of foraging behavior) (Table 1), where suitable caterpillars and orthopteran insects were available for both *Parus* species (Fig. 4). This foraging microhabitat would also be a useful food source for both *Parus* species.

In conclusion, both *Parus* species selectively used foraging microhabitats with different arthropod communities according to their species-specific size preferences. The composition of their diets may reflect both the characteristics of the arthropod community in each area and the abundance and size of prey items in each foraging microhabitat within each area.

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Prey distribution and foraging preference for tits

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Abstract We examined the abundance and distribution of prey in four different height strata and eight tree species in a temperate forest, and analyzed the influence on foraging preference by three breeding tit (*Parus*) species. Densities of arthropod prey for tits in canopy foliage varied with tree species but not with height. Most of them were Lepidoptera larvae. Also, interspecific differences in choice of foraging substrate were found between tree species but not in height. These results demonstrate that tree species composition is a more important habitat factor than foliage height profile for coexistence of different tit species in forests. We examined four different measures of prey abundance to find how tits chose tree species. The largest species, the Great Tit *P. major*, preferred the tree species with high total biomass, and the intermediate-sized Willow Tit *P. montanus* preferred those with high density per leaf area. Concentrated searching for prey on a few tree species with high total biomass may be a useful strategy for inflexible perch-gleaners such as *P. major*, and finer-scale searching on each leaf may be more practical for agile foragers such as *P. montanus* which often hang-glean to reach less accessible food. In spite of these differences, both species gained benefits from choosing the tree species on which they foraged most efficiently. In contrast, the smallest species, the Coal Tit *P. ater*, frequently foraged on food-poor tree species. Of the three tit species, *P. ater* was the most generalized forager, using diverse techniques on a variety of tree species and specializing at capturing small prey quickly. These foraging patterns may make it possible for the smallest species to coexist with the other tit species.

Key words Foraging efficiency, Foraging technique, *Parus*, Prey distribution, Tree species preference

As habitat factors determining bird species diversity in forests, some researchers have emphasized the importance of vertical foliage distribution (MacArthur & MacArthur 1961; Recher 1969) and others have emphasized tree species composition (Rice et al. 1984; Verner & Larson 1989). Either of these factors could help different species co-exist in different forests, and it remains unclear whether one or both factors provides a general mechanism for coexistence. Holmes et al. (1979) proposed a hypothesis that tree species composition determines bird species

diversity within guilds, the presence and size of which are determined by foliage height distribution. Hino (1985) supported this idea in part by a correlation analysis between habitat variables and bird communities in shelterbelts of Hokkaido, but we need to know how bird species partition height strata and tree species based on food availability in forests.

Many studies have shown the different use of height strata and/or tree species among insectivorous bird species within the same guild (Hartley 1953; MacArthur 1958; Morse 1970; Lack 1971; Alatalo 1982; Hino 1998). Few studies, however, have examined prey abundance and distribution although the need for such studies has been recognized for many years (Wiens 1984; Morrison et al. 1990). Holmes and his colleagues demonstrated that foraging by birds on three different tree species was influenced by the prey abundance on and foliage structure of each tree species and the species-specific ability of the

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birds (Holmes & Robinson 1981; Holmes & Schultz 1988). Their conclusion was somewhat speculative, however, because they examined only three species of trees. Moreover, the prey distributions and their effects on bird foraging at different height strata have never been studied in forest habitats.

In this paper, we examine the abundance and distribution of prey in four different height strata and eight tree species in a temperate forest, and analyze the influence on foraging preference by three breeding tit (*Parus*) species. We then reveal interspecific differences in the degree to which prey abundance determines foraging preference, and relate it to searching-pattern constraints on foraging techniques of each species.

METHODS

1) Vegetation

This study was conducted in the Nakagawa Experimental Forest of Hokkaido University, northern Hokkaido, Japan (44°49'N, 142°16'E). A 6-ha study plot (200 m × 300 m) was established along the mountain ridge (c. 350 m in altitude). This plot largely consists of deciduous broad-leaved trees dominated by *Quercus mongolica* and *Betula ermanii* with <10% of conifers *Picea jezoensis* and *Abies sachalinensis* (Appendix). Canopy height is 15–20 m. The understory is dominated by high density of two bamboo species *Sasa kurilensis* and *Sasa senanensis* 1.0–1.5 m in height.

Vegetation was surveyed in the study plot in July 1990. Species, numbers of individuals and DBH (diameter at breast height) were recorded for all trees > 5 cm in DBH. The relative importance value (IV) of each tree species was calculated as the percentage of basal area (the sum of cross sectional areas of trunks determined from DBH), which is closely correlated with leaf surface area (Holmes & Robinson 1981). To determine the foliage distribution (in percentage cover) at five different height strata (0–3.6 m, 3.6–7.2 m, 7.2–10.8 m, 10.8–14.4 m, 14.4 m+), four categories of foliage volume (0: none, 1: 1–33%, 2: 34–66%, 3: 67–100%) were recorded by eye at 459 points, averaged and multiplied by 30% for each stratum.

2) Insect distribution

All arthropods, most of which were Lepidoptera larvae (97.6% in dry weight), were collected and counted from 300 leaves per unit, and their body

lengths were measured in the laboratory. The dry weight (W, mg; 60°C, 48 h) of an arthropod was estimated from the body length (L, mm) with the following equation: $W = 0.033L^{2.52}$ ($r = 0.92$, $P < 0.001$, $N = 180$). This equation was determined with a part of the samples (W, mg). For statistical analyses, the dry weights were transformed to $\ln(W + 0.5)$ to reduce skewness.

The abundance of arthropods in the canopy foliage at different height strata was examined in June 1990. We collected samples directly from a nine-storied tower (14.4 m high and 10 m square) built of steel pipes near the study plot. This tower gave access to six trees of *Quercus mongolica* and seven of *Betula ermanii*, which were two dominant species. We chose two units randomly for arthropods sampling from each tree species at each story in June. The unit samples from both species were combined and averaged for each of the same height strata as foliage distribution except the 0–3.6 m stratum for which no foliage was accessible. The expected percentage of prey biomass at each height stratum was calculated based on the average dry weight multiplied by the foliage volume to compare with the foraging height use by birds.

The abundance of arthropods in the canopy foliage of different tree species was examined in June 1991. We collected samples from the branches 1–3 m in height with a clipping method. The tree species examined were the eight species >2% in IV (Appendix): *Quercus mongolica*, *Betula ermanii*, *Kalopanax pictus*, *Picea jezoensis*, *Abies sachalinensis*, *Tilia japonica*, *Acer mono* and *Phellodendron amurense*. We used four different measures of arthropod abundance as determinants of tree species selection by birds because the tree density and the leaf area varied among tree species. The two indices of density were the average dry weight (mg) per 100 leaves (D_a) and per 1 m²-leaf area (D_b), and the two indices of total biomass in the study site were $D_a \times IV$ (T_a) and $D_b \times IV$ (T_b), respectively. To calculate D_b , we collected 25 leaves randomly from three trees of each species and measured their areas with a digitizer. We treated one shoot with a node for two conifer species and one leaflet for *Phellodendron amurense* with compound leaves as one piece of leaf.

3) Bird foraging

Observations were made in the morning (0600–1100 hours) and in the afternoon (1400–1700 hours) in June and July 1990 and in June 1991. The target

species were three breeding tit species, Great Tit *Parus major*, Willow Tit *P. montanus* and Coal Tit *P. ater*, the densities of which were 21.7, 34.8 and 43.5 pairs/100 ha, respectively (Hino & Nakano 1992). Body size was largest in *P. major*, medium in *P. montanus* and smallest in *P. ater* (14.1 g, 10.7 g, 8.5 g in Nakamura 1978). Each time a bird was observed foraging for prey (including active searching), we recorded the height and tree species, and the prey length estimated in 5 mm intervals using beak size as a standard. We also differentiated between three types of feeding technique (perch-gleaning, hang-gleaning or sally-hovering; Remsen & Robinson 1990). To avoid bias from repeated observations of the same individuals, we collected data from individuals in different territories in the study area. In 1991, foraging time (searching and handling) was timed for each tree species. Foraging efficiency (mg/min) was calculated as a total dry weight of prey (estimated by body length) divided by the total foraging time for each tree species. Foraging rate was also calculated as the number of prey captured per minute.

Tree species preference was calculated with $\ln(r_i/p_i)$, where r_i was the proportion used by birds and p_i was the IV/100 for each tree species i . For the diversity of the tree species and feeding technique used by birds, we used the Simpson's diversity index: $1/\Sigma p_i^2$, where p_i was the proportion of a category i . Correlation analyses were conducted to reveal which indices of food abundance on different tree species were related to the preferences and the foraging efficiencies by each tit species. We considered $P < 0.1$ as significance level owing to small sample sizes (5–6).

Bird classification followed the Ornithological Society of Japan (2000)

RESULTS

1) Foraging height

In *Quercus mongolica* and *Betula ermanii* in 1990, the average dry weight of arthropods per 100 leaves was 32.2 mg (± 28.6 SD, $N=14$) in the canopy foliage >3.6 m in height. The dry weights did not differ significantly among four height strata ($F_{3,24}=0.72$, $P=0.55$), nor in comparisons between pairs of different strata (F-test with Bonferroni correction, $P>0.20$, Table 1). The foliage volume varied from 38% to 58% in percentage cover among height strata. The estimated biomass of prey was least in the top stratum (14.4 m+) and greatest in the stratum immediately below (10.8–14.4 m), with a threefold difference between the two values (Table 1). χ^2 -analyses revealed that the tit species all foraged made use of each stratum in proportion to the distribution of prey biomass in the study site, with no significant difference between species ($\chi^2=15.1$, $df=8$, $P>0.05$).

2) Foraging tree species

In 1991, the average dry weights of arthropods per 100 leaves (D_a) varied greatly among tree species from the lowest in *Picea jezoensis* through the highest in *Kalopanax pictus* (Table 2). However, the orders of each species changed when we used different indices of prey abundance. In terms of dry weight per 1 m² (D_b), the highest values were obtained for *Betula ermanii* and then *Tilia japonica*, with large-leaved,

Table 1. Prey abundance and foraging uses by tits at each height stratum

Height category (m)	Foliage (%)	Caterpillar biomass		Bird foraging use (%)		
		Dry weight per 100 leaves (mg) ¹	Expected biomass (%) ²	<i>P. major</i>	<i>P. montanus</i>	<i>P. ater</i>
14.4–	38.6	22.0 \pm 13.9 (4)	14.1	6.3	13.1	25.0
10.8–14.4	58.1	43.7 \pm 44.0 (8)	42.1	37.5	33.8	32.4
7.2–10.8	55.8	25.1 \pm 15.5 (8)	23.2	29.2	26.2	19.4
3.6–7.2	38.1	32.8 \pm 18.3 (8)	20.7	27.1	22.8	17.6
0–3.6	57.2	–	–	0.0	4.1	5.6
No. of observations				48	145	108
χ^2 -value ($df=3$) ³				6.63	5.17	5.16

¹ Mean \pm SD (no. of sample size).

² Percentages based on (Dry weight per 100 leaves) \times (Foliage %) in the height categories 2–5.

³ Comparisons of bird foraging use to expected prey biomass in the height categories 2–5. Neither values were significant ($P>0.05$).

Table 2. Four indices of prey abundance on each tree species

Tree species	D _a : Dry weight per 100 Leaves (mg)	D _b : Dry weight per 1 m ² (mg)	T _a : Total biomass D _a ×IV ¹	T _b : Total biomass D _b ×IV ¹
QM	27.7	36.9	977.5	1303.4
BE	99.0	293.0	3089.5	9140.6
KP	182.4	137.4	1312.9	989.4
PJ	2.8	10.3	13.2	49.3
AS	11.3	47.7	38.3	162.3
TJ	71.7	155.0	186.5	402.9
AM	29.3	53.9	61.5	113.1
PA	7.4	35.6	14.9	71.2

¹ Importance Values (%) in Appendix.**Table 3.** Foraging uses and preferences of tits on each tree species

Tree species	<i>P. major</i>		<i>P. montanus</i>		<i>P. ater</i>	
	Use (%)	Preference	Use (%)	Preference	Use (%)	Preference
QM	28.0	0.26	15.1	-0.07	26.0	0.21
BE	50.0	0.74	50.0	0.74	28.0	0.33
KP	8.0	0.48	9.3	0.58	0.0	-0.69
PJ	2.0	-0.69	0.0	-0.69	18.0	1.45
AS	0.0	-0.69	8.1	1.06	10.0	1.24
TJ+AM+PA	6.0	0.35	11.6	0.80	12.0	0.83
No. of observations	50		86		50	
Simpson's diversity	2.94		3.36		5.15	

Kalopanax pictus (Appendix) falling to third place. Indices of total biomass (T_a and T_b), as expected, were high in the two dominant species, *Betula ermanii* and *Quercus mongolica* (>30% in IV, Appendix).

Tree species preferences for foraging differed among tit species (Table 3). *P. major* foraged on the lowest diversity of tree species, preferring *Betula ermanii* and avoiding conifers. *P. montanus* showed opposing preferences for each of the two coniferous species, preferring *Abies sachalinensis* and avoiding *Picea jezoensis*. *P. montanus* also made preferential use of deciduous species except *Quercus mongolica*. *P. ater* foraged on the greatest diversity of tree species, but showed special preferences for each of the two coniferous species and avoided *Kalopanax pictus*. Foraging efficiencies on each tree species also differed among the tit species (Table 4). *P. major* captured prey on *Betula ermanii* and *Quercus mongolica* most effectively. *P. montanus* did so on *Betula ermanii* and *Kalopanax pictus*, and *P. ater* on *Acer mono*.

Correlation analyses were conducted to reveal which indices of food abundance on different tree species (Table 2) were related to the preferences (Table 3) and foraging efficiencies (Table 4) of each tit species (Table 5). *P. major* foraged preferentially on the tree species with high total biomass in the study site (T_a and T_b). *P. montanus* foraged preferentially on tree species with high dry weight per leaf area (D_b). In both species, the indices of prey abundance for the tree species where they foraged most efficiently were consistent with those they preferred, although this relationship was not significant (Table 5). On the other hand, *P. ater* did not show positive relationships with any of the indices, but tended to avoid foraging on the tree species with high values of D_a and T_a (Table 5).

3) Foraging technique

P. major was a specialized perch-gleaner, *P. montanus* foraged most frequently by hang-gleaning, and *P. ater* used both perch- and hang-gleaning with the same frequency. The diversity of foraging techniques

Table 4. Foraging efficiencies of tits on each tree species

Tree species	<i>P. major</i>		<i>P. montanus</i>		<i>P. ater</i>	
	Efficiency (mg/min)	Time (sec)	Efficiency (mg/min)	Time (sec)	Efficiency (mg/min)	Time (sec)
QM	28.6	457	5.5	384	14.4	672
BE	34.9	1185	46.4	1241	12.0	748
KP	21.9	83	44.3	265	—	—
PJ	0.0	36	—	—	4.9	253
AS	—	—	21.9	219	5.9	97
TJ+AM+PA	5.0	201	36.1	409	49.2	162
All species	28.9	2018	34.7	2631	14.8	1932

Table 5. Results of correlation analyses between foraging preferences (Table 3) or efficiencies of tits (Table 4), and four indices of caterpillar abundance on each tree species (Table 2)

	N	D _a	D _b	T _a	T _b	Preference
Preference						
<i>P. major</i>	6	NS	NS	+	(+)	
<i>P. montanus</i>	6	NS	(+)	NS	NS	
<i>P. ater</i>	6	—	NS	—	NS	
Efficiency						
<i>P. major</i>	5	(+)	NS	+	+	(+)
<i>P. montanus</i>	5	NS	(+)	NS	NS	NS
<i>P. ater</i>	5	NS	NS	NS	NS	NS

Positive correlation: + $P < 0.05$, (+) $0.05 < P < 0.1$; Negative correlation: — $P < 0.05$; NS: $P > 0.1$.

N: sample size.

Table 6. Foraging techniques of tits

Foraging technique	<i>P. major</i>	<i>P. montanus</i>	<i>P. ater</i>
Perch-gleaning	85.4	23.3	41.9
Hang-gleaning	2.4	58.3	40.0
Sally-hovering	12.2	18.3	18.1
Number of observations	41	120	105
Simpson's diversity	1.34	2.33	2.71

was highest in *P. ater* and lowest in *P. major* (Table 6).

In total, foraging efficiency was high in *P. montanus* and *P. major*, and low in *P. ater* (Table 4). This difference was related to prey size captured by each tit species: *P. ater* caught significantly smaller prey ($9.0 \text{ mg} \pm 20.4 \text{ SD}$, $N=53$) than *P. montanus* ($23.8 \text{ mg} \pm 35.4 \text{ SD}$, $N=64$, U-test with Bonferroni's correction: $z = -3.21$, $P < 0.05$) or *P. major* ($27.8 \text{ mg} \pm 40.8 \text{ SD}$, $N=35$, $z = -2.62$, $P < 0.005$). On the con-

trary, foraging rate was highest in *P. ater* (1.65), the second in *P. montanus* (1.46) and lowest in *P. major* (1.04). The species with the most diverse technique took prey at the fastest rate ($r=0.99$, $P < 0.05$, $N=3$).

DISCUSSION

During the breeding season, densities of arthropod prey for tits varied with tree species but not with height. The three tit species showed interspecific differences in their use of tree species but not in use of height. These quantitative results demonstrate that tree species composition is a more important habitat factor than foliage height profile for coexistence of different tit species in forests. Similar results were found by Holmes et al. (1979) in North American forests and by Hino (1985) in northern Japanese shelterbelts. These studies show that tree species composition determines bird species diversity within guilds, though abundance may be affected further by foliage height distribution.

Our results suggest that each tit species responded to a different measure of prey abundance in selecting tree species for foraging. The largest species, *P. major* preferred the tree species with high total biomass in a forest, and the intermediate-sized, *P. montanus* preferred those species with high average density per leaf area. This interspecific difference may be related to their searching patterns associated with foraging technique. *P. major* was a specialized perch-gleaner taking prey mainly from the upper surface of leaves, as reported in other studies (Morse 1978; Hino 1993). *P. montanus* hang-gleaned more frequently but also foraged by perch-gleaning and sally-hovering. Since most of caterpillars are found on undersides of leaves (Greenberg & Gradwohl 1980; Holmes & Schultz 1988), hang-gleaning would be a

more effective (but energy-expensive) technique for birds to access them. Thus, *P. montanus* are expected to forage on different tree species more flexibly than *P. major* while searching for prey from tree to tree, as indicated by using more diverse species of trees and fine-scale searching on each leaf. On the other hand, concentrated searching for prey on a small number of tree species with high total biomass may be useful for less flexible perch-gleaners like *P. major* because prey accessibility is constrained (Holmes & Robinson 1981; Holmes & Schultz 1988). In spite of these differences, both species gained benefits from choosing the tree species where they foraged most efficiently (as reported by Partridge 1976a, b).

In contrast, the smallest species, *P. ater* often used food-poor tree species. We can suggest two possible reasons to explain this observation. One possibility is that interference competition from the larger species may deny *P. ater* access to the most profitable foraging sites. Many studies have shown that *P. ater* are forced to food-poor substrates in the presence of the other tit species (Alatalo et al. 1985; Alatalo & Moreno 1987; Suhonen et al. 1993; Fyhn & Sorensen 1997). These studies all were conducted in winter when interspecific competition was severe owing to scarcity of food resources. Our study indicates that interspecific competition may also play an important role for foraging-site selection by tits during the breeding season. The other possibility is that *P. ater* with a morphology adapted to conifers (Partridge 1976b), may forage on *Picea jezoensis* and *Abies sachalinensis* frequently regardless of prey abundance. This could be partly true but *P. ater* was neither a specialized nor an efficient forager on conifers. Goldcrests *Regulus regulus*, which also bred in low density in the study site (4.3 pairs/km², Hino & Nakano 1992), are known as specialized foragers in conifers (Nakamura 1980). This species foraged on coniferous trees much more frequently (83% in 1990, 55% in 1991) and more efficiently (20.4 mg/min) than *P. ater*, with more frequent sally-hovering (56%) (Hino et al. unpubl. data). Of the three tit species, *P. ater* was the most generalized forager. This species took prey from a variety of tree species with diverse foraging techniques: by perch-gleaning like *P. major*, hang-gleaning like *P. montanus* and sally-hovering like *Regulus regulus*. Instead of low foraging efficiency, *P. ater* captured small prey with high speed. This flexible foraging pattern may make it possible for this smallest tit species to coexist with the other tit species.

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Appendix Average leaf area (\pm SD, N=25) and importance value (IV) of each tree species

Code	Tree species	Leaf area (cm ²)	Importance value (%)
QM	<i>Quercus mongolica</i>	75.0 \pm 49.5	35.3
BE	<i>Betula ermanii</i>	33.8 \pm 12.1	31.2
KP	<i>Kalopanax pictus</i>	132.7 \pm 106.1	7.2
PJ	<i>Picea jezoensis</i>	26.8 \pm 12.3	4.8
AS	<i>Abies sachalinensis</i>	23.6 \pm 15.9	3.4
TJ	<i>Tilia japonica</i>	49.3 \pm 19.7	2.6
AM	<i>Acer mono</i>	54.4 \pm 26.4	2.1
PA	<i>Phellodendron amurens</i>	20.9 \pm 14.1	2.0

The effects of food-supply on Southeast Asian forest birds

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Abstract Southeast Asian forests are being lost at an alarming rate. This unprecedented deforestation is resulting in avifauna losses. Despite this, Southeast Asian avifauna remains poorly studied. A few studies measured the food-supply and correlated it with the Southeast Asian forest bird ecology. These correlative studies (qualitative as well as quantitative) show that food-supply can affect the bird diversity, abundance/density, breeding ecology, body condition, ranging behaviour and/or flocking behaviour. However, there has been no experimental study conducted to determine the effects of food-supply on the forest bird ecology. In this geographic area, exciting research avenues remain available to study the avian feeding ecology and to explore a relationship between food-supply and forest bird ecology. Descriptive, correlative as well as experimental data on these aspects are required to enhance the knowledge of avian ecology as well as for avian conservation purposes.

Key words Bird ecology, Food-supply, Rainforest birds, Southeast Asia, Tropics

Southeast Asia (primarily containing Myanmar, Thailand, Cambodia, Laos, Vietnam, Malaysia, Singapore, Brunei and Indonesia) is a region of high bird diversity with over 1200 bird species present (Inskipp et al. 1996, Robson 2000). Within this region, at least 70% of resident bird species may be partly or exclusively dependent upon the primary forest (Wells 1985). The percentage of threatened species restricted to forested areas within Southeast Asia varies from 17% (Singapore) to 72% (Indonesia) (Collar et al. 1994). Despite this, forest loss in Southeast Asia has been extensive; with rate of deforestation three times higher here than other tropical areas (Food and Agriculture Organization 1999). This forest loss has probably resulted in concomitantly heavy avian extinctions (Diamond et al. 1987, Castelletta et al. 2000).

The avian extinctions do not appear to occur randomly following forest loss (e.g. Karr 1980, Brash 1987). Frugivores and insectivores, for example, are particularly vulnerable to extinctions after deforestation (Castelletta et al. 2000). One of main contributing factors in such cases could be a decline in food-supply. Therefore, it may be critical to understand the relationships between the ecology of forest birds (de-

pending on primary or old secondary forest to survive) and food abundance/density. My objectives here are to: 1) summarize results of studies exploring food-supply and bird ecology relationships, 2) identify if there are any general patterns based on previous studies and 3) provide some future directions for studies to determine the effects of food-supply on bird ecology. Only studies where food abundance/density was quantitatively measured and related with Southeast Asian bird ecology are discussed here. Published studies were searched by using various databases such as the Web of Science and BIOSIS. These searches were supplemented by gleaning through the literature cited by relevant studies and searching through some of the regional journals such as *Tropical Biodiversity*. Bird classification used in this manuscript follows Sibley & Monroe (1990).

CASE STUDIES

1) Malaysia

Fogden (1972) estimated fruit and insect abundance in the Semengo Forest Reserve (Sarawak, Malaysia). He qualitatively related the food abundance with various aspects of bird ecology. Birds' breeding in December to May coincided with a period when insects were more abundant. Frugivorous

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bird species had similar breeding phenology as insectivorous bird species despite the fact that fruits were not consistently abundant during any particular time of the year. This may be due to the fact that many frugivorous species supplement their diets with protein rich insects during the breeding season.

In Semengo, insects were least abundant in November and most bird species finished moulting by the end of October (Fogden 1972). Exception to this included the species for which insect abundance was suspected not to vary widely such as bark-foraging woodpecker species (e.g. the Rufous Woodpecker *Celeus brachyurus*) and leaf-litter foraging babbler species (e.g. the Short-tailed Babbler *Malacocincla malaccensis*).

Two bulbul species (*Pycnonotus* spp.) in Semengo fed on both insects as well as fruits (Fogden 1972). Fruits must have constituted an important part of the diet for these bulbuls because they consumed them even when insects were plentiful. Probably fruits represent an easily harvestable source of energy. These two bulbul species had suppressed breeding activity in low fruit abundance year than in high fruit abundance year. The proportion of juveniles in the population was seven fold higher in high fruit abundance year (14%) than in low fruit abundance year (2%). There also seemed to be a recovery in the body masses of these bulbul species when fruits abundance increased (Fogden 1972). Thus, Fogden's qualitative study implies broad consequences of food-supply on the bird ecology.

Wong (1986) studied the effect of food resources (flowers, fruits and arthropods) on understory bird communities in primary versus disturbed (regenerated) areas of the Pasoh Forest Reserve (Peninsular Malaysia). Wong found that the number of plant individuals that produced flowers or fruits used by birds was at least three times higher in primary than in the disturbed forest. Foliage arthropod abundance did not differ between the primary and disturbed areas but the period of low arthropod abundance was four months longer in disturbed than in the primary forest. Both, bird species richness (73 versus 83 species) and abundance (575 versus 703 individuals), were lower in disturbed than in the primary forest. Wong argued that this was because lower resource abundance could support fewer birds in disturbed than in the primary forest.

In Pasoh, foliage arthropods did not show marked temporal and spatial variation as shown by fruiting and flowering plants. Therefore, frugivores would

have to range over wider areas than insectivores. Consistent with this prediction, Wong (1986) found that the abundance of frugivores varied twice more than that of insectivores both in primary and the disturbed forest. Wong's study highlights the importance of food-supply on the avian community diversity and abundance.

2) Indonesia

Leighton and Leighton (1983) monitored fruit density in the Kutai Nature Reserve (Kalimantan, Indonesia). In a semi-quantitative manner, they correlated fruit density with frugivore behaviour and movements. Leighton and Leighton found that all hornbill species (the Rhinoceros Hornbill *Buceros rhinoceros*, Helmeted Hornbill *Rhinoplax vigil*, Bushy-crested Hornbill *Anorrhinus galeritus*, Black Hornbill *Anthraceros malayanus*, White-crowned Hornbill *Aceros comatus*, Wrinkled Hornbill *A. corrugatus* and Wreathed Hornbill *A. undulates*) only bred when the fruit density peaked (January to May). Based on bird sightings, it appeared that the Green Imperial Pigeon *Ducula aenea*, Jambu Fruit Dove *Ptilinopus jambu*, Hill Myna *Gracula religiosa*, Green Broadbill *Calyptomena viridis*, *A. undulates* and *A. corrugatus* emigrated from the study area during low fruit density periods (September-October). These results suggest that birds may be adjusting their breeding activities and/or foraging areas by tracking food resources.

Kinnaird et al. (1996) studied the effect of temporal and spatial differences in fruit abundance on the Sulawesi Red-knobbed Hornbill (*Aceros cassidix*) in the Tangkok DuaSundra Nature Reserve (Sulawesi, Indonesia). The Sulawesi Red-knobbed Hornbill feeds on fruits in the forest canopy. Kinnaird et al. (1996) found that fig (*Ficus* spp.)-fruit biomass correlated significantly with the temporal population fluctuations of the hornbill. The flock size also increased during months when fig-fruit biomass was high. Additionally, hornbill densities were higher in areas with higher than in lower fig-tree densities (Kinnaird et al. 1996). In line with some previous studies (e.g. Wong 1986), food-supply seemed to effect population dynamics in this case.

3) Singapore

Sodhi et al. (in press) studied the effects of food abundance on bird abundance in two large (>480 ha) forest fragments, MacRitchie and Nee Soon, in Singapore. Line transects of approximately four and half

km were surveyed eight times at each site between 14 July and 24 September 1997. All surveys were made during fair weather conditions and between 0700 and 0930 h. Foliage along the transects was sweep sampled for the presence of understorey arthropods. Each transect was sampled for arthropods on five different occasions. Sweep sampling was conducted at intervals of 150 m and 16 sweeps using butterfly net were made at each sampling station. Sampling stations were changed for subsequent samplings. All arthropods found were used in calculating their mean abundance. The number of fruiting trees along the transect was also counted twice.

Sodhi et al. found that the mean number of understorey insectivore bird individuals (belonging to species: the White-rumped Shama *Copsychus malabaricus*, Dark-necked Tailorbird *Orthotomus atrogularis*, Abbott's Babbler *M. abbotti*, Short-tailed Babbler and Chestnut-winged Babbler *Stachyris arthroptera*) did not differ significantly between MacRitchie (73.63 ± 5.76 [standard error] individuals) and Nee Soon (87.88 ± 7.57 individuals). And as expected, the mean number of foliage arthropods also did not differ between the two forests (11.8 ± 0.39 [standard error] and 9.66 ± 0.67 individuals, respectively). However, more frugivore bird individuals (belonging to species: the Red-crowned Barbet *Magalaima rafflesii*, Long-tailed Parakeet *Psittacula longicauda* and Pink-necked Green-Pigeon *Treron vernans*) were found in MacRitchie (maximum number=45) than in Nee Soon (10). More fruiting trees were also available in MacRitchie (maximum number=352) than in Nee Soon (285).

Castelletta (unpubl. data) measured the arthropod abundance and insectivore bird density in 13 forest patches (7–935 ha) in Singapore. Eleven insectivorous bird species that feed in the understory were considered (the Laced Woodpecker *Picus vittatus*, Oriental Magpie Robin *Copsychus saularis*, White-rumped Shama, Yellow-bellied Prinia *Prinia flaviventris*, Common Tailorbird *Orthotomus sutorius*, Dark-necked Tailorbird, Rufous-tailed Tailorbird *O. sericeus*, Ashy Tailorbird *O. ruficeps*, Abbott's Babbler, Chestnut-winged Babbler and White-chested Babbler *Trichastoma rostratum*). Castelletta analysed correlations between the mean insectivore density (all species combined) and all arthropod abundance. Separate analyses were conducted for arthropods less than 1 cm and those more than 1 cm in length. No significant correlation was found between the mean density of insectivores and arthropod abundance for all

the comparisons. One of the reasons for this lack of correlation may be that the diet of the study species is poorly understood thus making the analyses crude. However, Castelletta found that arthropod abundance was highest during the peak of the breeding season (April to September) of insectivorous forest birds. The studies from Singapore show that some food types can effect bird abundances and breeding season while others may either exert minimal effect or their effect may be difficult to demonstrate.

WHAT ARE THE GENERAL PATTERNS?

Only a few studies have been conducted on the effects of food-supply on Southeast Asian forest birds. However, these limited number of studies imply the importance of food-supply on forest bird ecology (Table 1). Timing of breeding and moulting, bird diversity and abundance/density, ranging behaviour and flock size seem to be effected by food-supply. The only study that found no significant correlative effect of food-supply on forest bird abundance is from Singapore (Castelletta unpublished data). As mentioned, this study suffers from the fact that the diet of the studied bird species remained poorly documented. Some of the studies also imply or show that different prey types exert different influences on the bird ecology. Arthropod resources usually do not show remarkable temporal and spatial variation in abundance as shown by other resource types such as fruits and flowers. The temporal and spatial variation in the abundance of fruits particularly effects the distribution, dispersal and movements of the frugivores (e.g. Fogden 1972, Wong 1986, Kinnaird et al. 1996).

FUTURE DIRECTIONS

One of the problems with Southeast Asian forest birds is that basic descriptive data are lacking even to conduct critical correlative studies. For example, the diet composition of many birds is poorly understood and data on breeding ecology (e.g. clutch sizes) are not readily available.

All the studies determining the effects of food-supply on Southeast Asian forest birds are either qualitative or at the best correlative. Demonstrating a precise effect of food-supply on bird ecology may be difficult from correlative studies and there may be a need to conduct well-designed experiments (Newton 1998). Correlative studies do however, present hypotheses and ideas for experimental testing. As men-

Table 1. The number of studies correlating the food-supply with Southeast Asian forest bird ecology.

Bird ecology	Total no. of studies	No. of studies with quantitative comparisons	No. of studies with experimental evidence
Population characteristics			
Diversity	1	1	0
Abundance/density	4	4	0
Breeding ecology			
Phenology	3	0	0
Reproductive success	1	0	0
Other ecological aspects			
Body condition	1	0	0
Moulting	1	0	0
Flocking	1	1	0
Ranging behaviour	2	0	0

tioned, even correlative studies linking the food-supply with Southeast Asian forest bird ecology are few. There is an urgent need to conduct the studies that attempt to find a correlation between food supply and bird movements, reproductive success and recruitment. With relatively well-developed radio-tracking techniques, it is now possible to track selected bird species and determine how they use home ranges or territories in relation to food distribution.

Mass flowering or fruiting is a striking feature of dipterocarp forests of Southeast Asia (Ashton et al. 1988). This phenomenon occurs during irregular intervals of 2–10 years and it causes many different families to flower simultaneously. While the ecological causes of this phenomenon are poorly understood (Corlett 1990), such an event can have profound impacts on bird ecology and adaptations. To my knowledge, the effects of mass flowering or fruiting on Southeast Asian forest bird ecology remains poorly documented.

To my knowledge no experimental study has been conducted to determine the effects of food-supply on Southeast forest birds (Table 1). For some of the relatively well-studied species, food supplementation (e.g. addition of fruits to a frugivore's range) or food reduction (e.g. removing or killing of exotic vegetation) experiments should be carried out. Therefore, in summary, exciting research avenues remain available on the feeding ecology and on the effects of food-supply on Southeast Asian forest bird ecology. In light of heavy deforestation, descriptive, correlative as well as experimental data are urgently needed on these research aspects. Researchers can rely for theoretical and methodological considerations on the re-

search conducted on the effects of food-supply on forest birds in other geographic areas (e.g. Holmes & Schultz 1988, Rodenhouse & Holmes 1992, Burke & Nol 1998).

CONCLUSIONS

As mentioned, forests within Southeast Asia are lost at an unprecedented rate. Previous studies reveal that forest loss and fragmentation can cause local extinctions in birds in this region (e.g. Ford & Davison 1996, Castelletta et al. 2000). Despite this, the ecology of Southeast Asian forest birds remain poorly studied. Because reduction in food-supply may be one of the variables causing the decline or local extinction of Southeast Asian forest birds, it is critical to understand the relationships between food-supply and bird ecology. Avian extinctions may occur over 100 years following habitat loss (Brooks et al. 1999). Therefore, following habitat loss and degradation, there may be time to save some of the avifauna through proper conservation actions. For example, some of the supplemental food experiments may be critical to determine if the conservation of some of the threatened birds is feasible (e.g. maintaining or increasing their abundance with supplemental food).

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ORIGINAL ARTICLE

Spotted-throat individuals of the Rufous Vanga *Schetba rufa* are yearling males and presumably sterile

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Abstract The Rufous Vanga *Schetba rufa* is endemic to Madagascar and lives in one-female groups. During the 1994–1999 breeding seasons, a total of 294 nestlings were banded. Among these nestlings, 51 stayed within the study area as spotted-throat individuals. In the next breeding seasons, 35 of 45 spotted-throat individuals were subsequently observed as black-throated males, and once they became black-throated males, these individuals never reverted to the previous spotted-throat pattern. In contrast, 30 banded nestlings were recovered as yearling females with white throats, and the female's color pattern never changed thereafter. All the spotted-throat males were helpers or floaters. All the males of one group consisting of an adult male with a black throat and two males with spotted throats were captured and sacrificed humanely. The testes were dissected from each specimen and were histologically examined. The testes of the spotted-throat males contained only spermatogonia, and no spermatids or spermatozoa were present. In contrast, the testes of the black-throated male were well-developed and contained enlarged seminiferous tubules with lumen, where numerous spermatozoa were evident. Considering these facts, spotted-throat males of this species are assumed to be sterile. We suggest that, due to their underdeveloped testes, the spotted-throat males (one-year-old males) of the Rufous Vanga are physically incapable of breeding.

Key words Cooperative breeding, Delayed maturation, Madagascar, Plumage, *Schetba rufa*

The family Vangidae is monophyletic and underwent extensive *in situ* radiation in Madagascar (Yamagishi et al. 2001). The Rufous Vanga *Schetba rufa* is a member of this family. In a previous paper (Yamagishi et al. 1995) we reported that this endemic species lives in groups of two to four individuals and that the groups contain one adult female, one or two adult males and sometimes also an individual with a spotted throat. We described how those birds with spotted throats helped the pairs with brood care during part of the breeding cycle, and suggested that these individuals were immature males. In the present study we confirmed that individuals with spotted throats were yearling males.

Furthermore, we report that the spotted-throat males never attempted to copulate nor became breed-

ers. These observations implied that they had not reached sexual maturity. Was this absence of breeding in one-year-old males due to an inability of reproduction or to ecological constraints? The alternatives would lead us to different interpretations of delayed dispersal of yearling males. To answer the question of sexual maturity of yearling males, we here provide evidence concerning the change in plumage pattern of males and also provide anatomical evidence of spermatozoa maturation. From this viewpoint we then discuss the reproductive ability of helper males of this species.

STUDY AREA AND METHODS

A study of Rufous Vanga ecology and behavior was conducted at Botanical Garden A in the Ampijoroa Forest Reserve (16°15'S, 46°48'E, c. 200 m asl) about 110 km southeast of Mahajanga in Mada-

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gascar. We marked nestlings with individually distinct combinations of color bands during 1994–1999. Then, every breeding season from 1995 to 2000 we recorded which groups each individual joined, its status in the groups, and the color patterns of its throat.

On 15 October 1998, we captured all the males of a group consisting of an adult male with a black throat and two males with spotted throats (spotted-throat males 1 and 2). At that time of year, the captured group was at the late stage of nest-building, at which time we considered that the testes of adult males had achieved full functional maturity. After capture, birds were sacrificed humanely, body mass was measured with an electric balance to the nearest 0.1 g and wing length was measured with a ruler to the nearest 0.1 mm. At the field station the testes were dissected from each specimen, and fixed in 10% formalin solution until histological examination. Right and left testes from each bird were weighed to the nearest 0.1 mg with an electric balance. Each testis was subjected to standard histological procedures for light microscopy; the testis was embedded in paraffin, and sectioned at 4 μ m, the sections then stained with hematoxylin and eosin.

RESULTS

Among the 259 groups recorded during the seven years of study, 161 (62%) were pairs without male helpers, and 98 groups (38%) had one to four male helpers. Among the 98 groups containing helpers, 54 (55%) contained at least one male with a spotted throat. During the 1994–1999 breeding seasons, we banded a total of 294 nestlings, of which 51 stayed

within the study area as spotted-throat individuals (Fig. 1-a and Table 1). In the next breeding seasons, 35 of 45 spotted-throat individuals were subsequently observed as black-throated males (Fig. 1-b), and once they became black-throated males, they never reverted to the previous spotted-throat pattern (Table 1). In contrast, 30 individuals banded as nestlings were recovered as yearling females with white throats (Fig. 1-c) in the pre-breeding season or in the breeding season (some of them disappeared after the recovery). The female's color pattern never changed thereafter.

All the spotted-throat males were helpers or floaters. In general, after a male developed a black throat, he established a new territory and became a breeder. Of those 24 males whose age at first breeding was confirmed, 15 bred at two years old. During seven years of observations, we also noted seven instances where individually identifiable helper males with black throats attempted sneak copulations with breeding females. Of these incidents, in three cases the sneaking males were three years old, in two cases the same two-years-old male attempted mating, and in the remaining two cases the ages of the males were unknown. Furthermore, in the case of the two-years-old male, at least one nestling which the helping male cared for did not have an allele derived from the breeding male on a microsatellite locus developed as markers of paternity tests (Asai et al. 1999), but shared another allele with the helping male which attempted mating (Asai unpubl. data). We never observed males with spotted throats attempting to copulate with females, nor did we find them forming a pair. These observations suggest that the helper status

Table 1. Observed male nestlings within the study area and change of their throat color.

Year	No. nestlings banded	Observed individuals					
		1995	1996	1997	1998	1999	2000
1994	14	2	2	2	2	2	2
1995	38		8	7	7	6	3
1996	68			15	12	10	6
1997	53				10	7	7
1998	76					10	7
1999	45						6
Total	294						

Schadowed numbers indicate spotted-throat males.

of a black-throated male per se does not inhibit his reproductive activity. In comparison, among 21 yearling females observed in our study site during the

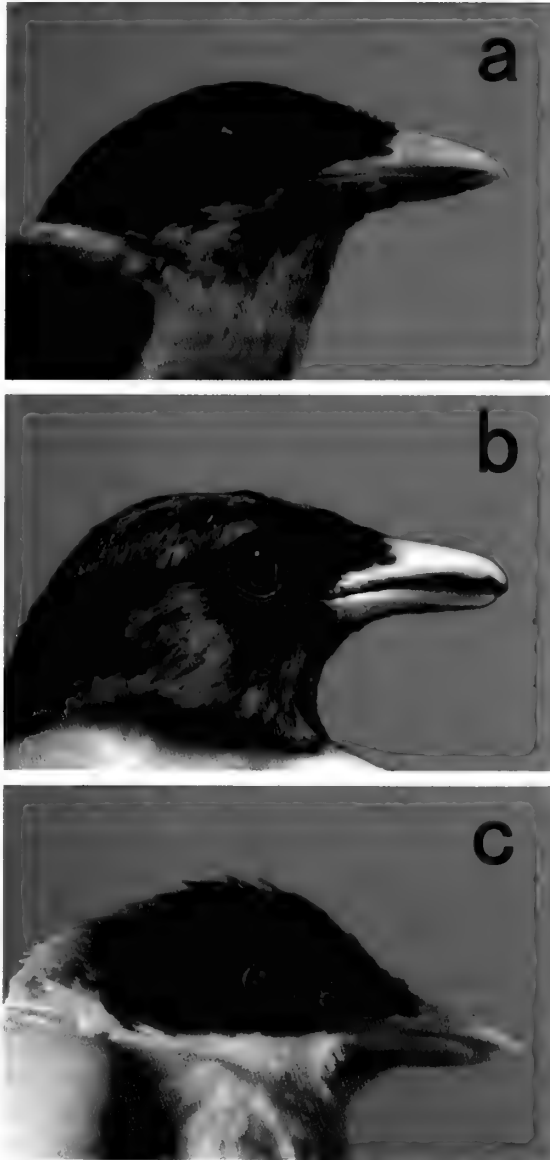


Fig. 1. The plumage of the head and throat in Rufous Vangas. a: a male with a spotted throat, b: a male with black throat, and c: a female.

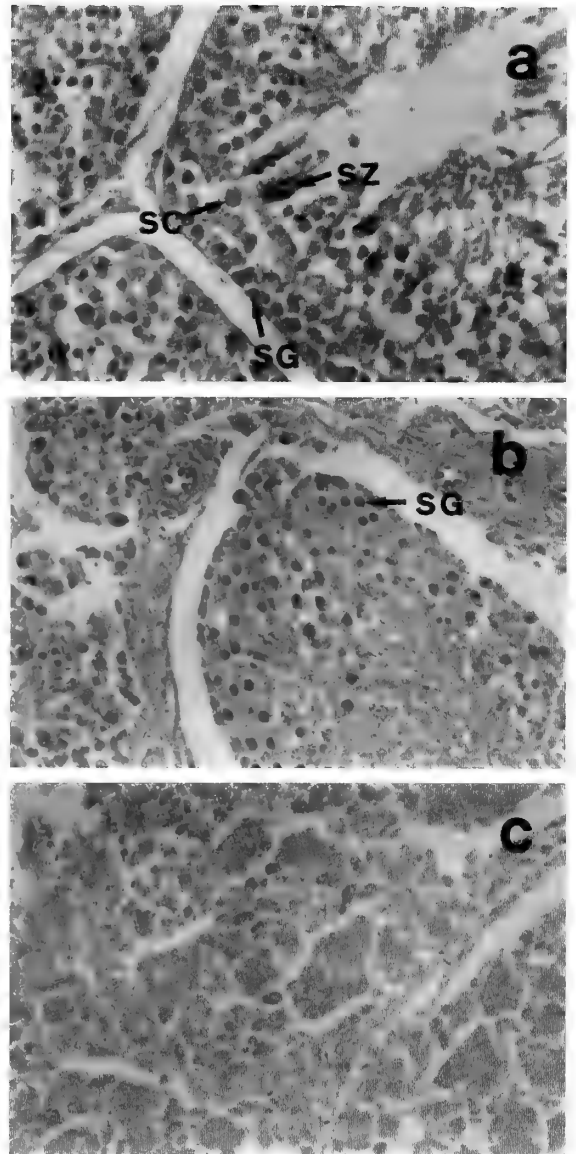


Fig. 2. Testis showing seminiferous tubules of three Rufous Vangas from the same breeding group, captured at the study site at the late nest-building stage. a: Black-throated male, b: Spotted-throat male 1, and c: Spotted-throat male 2. Note that spermatozoa were only found in the black-throated male. SG: spermatogonium, SC: spermatocyte, SZ: spermatozoa.

Table 2. Combined testes mass and right testicular volume of each Rufous Vanga captured at the late nest-building stage.

	Body mass (g)	Wing length (mm)	Tarsus length (mm)	Combined tested mass (mg)	Right testicular volume (mm ³)
Black-throated male	37.6	108.7	24.3	171.5	75.4
Spotted-throat male 1	39.4	103.9	24.4	60.8	38.5
Spotted-throat male 2	39.8	105.6	23.8	14.5	13.1

breeding season, 16 (76%) were breeders and 5 (24%) were auxiliary females.

Table 2 shows the combined testicular mass and measurements of body mass, wing length and tarsus length for each of the three dissected males. Histological pictures of testis sections are given in Fig. 2. When these pictures are considered together with the data of testicular mass, it is indisputable that the spotted-throat male 2 was an immature individual with completely regressed testes. The spotted-throat male 1 had heavier testes than spotted-throat male 2, but histological examination indicated that spermatogenesis in this individual had been arrested at the early stages. The testes contained only spermatogonia, and no spermatids or spermatozoa were present (Fig. 2-b). In contrast, the testes of the black-throated male were well-developed and contained enlarged seminiferous tubules with lumen, where numerous spermatozoa were evident (Fig. 2-a). This histological evidence indicates that the black-throated male was reproductively active, whereas the two spotted-throat males were not.

DISCUSSION

The observations that spotted-throat males never attempted to copulate nor became breeders, and that helper males of age two years or more could potentially copulate with females suggest that sexual maturity of males is not dependent on social constraint with respect to the helper status, but is instead age related. However, observational field data cannot strictly identify whether it is physiological restraint of maturity or ecological constraint on chance of mating which resulted in the absence of mating by the yearling males. In this context, although the direct evidence is lacking in black throat helpers, our anatomical evidence is more informative.

Morphological characters of the three sacrificed males were identical (Table 2), indicating that all had achieved mature adult size. However, testicular masses were different; only the black-throated male had mature testes, whereas the two yearling males with spotted throats had small regressed testes.

The testicular masses were different between two yearling males (Table 2). Unfortunately, we have insufficient data to explain the individual difference of testicular masses between these two yearlings. Such a difference, considering that these were immature individuals, might fall within the range of individual variations related to physiological conditions, or

might result from ecological constraints that acted to either advance or inhibit the developmental process of testes. In the former case, the difference of testicular masses might not be functional. In the latter case, the development of testes might correlate with the extent of helping activity of yearling males (cf. Eguchi et al. in press). However, even if the difference of testicular masses affected helping behavior, the anatomical data indicated clearly that the yearling males had not reached sexual maturity (Fig. 2).

Related helper males of the cooperatively breeding African White-browed Sparrow Weaver also have smaller testes (around 100 mg) than breeding males (>300 mg) in January/February (Wingfield et al. 1991). In this species, plasma levels of luteinizing hormone and testosterone in the helpers are also lower than in breeding males, indicating that helpers are not fully mature. Similarly, in the cooperatively breeding Florida Scrub-jay, helpers are subordinate and nonbreeders, and have smaller testes than the breeding males, with whom they share a territory (Schoech et al. 1996).

Suppression of hormonal levels of helpers is known in several cooperative breeding species (Schoech et al. 1996; Wingfield et al. 1991; Poiani & Fletcher 1994; Mays et al. 1991). However, whereas those studies emphasized the role of spontaneous restraint by subordinates, we suggest that, due to their underdeveloped testes, the spotted-throat males (one-year-old males) of the Rufous Vanga are physically incapable of breeding.

In the cooperatively breeding Mexican Jay, yearling males also never breed, and have low reproductive steroid levels during the breeding season (Vleck & Brown 1999). Two-year-old males do regularly breed whether or not they are nest owners. Vleck and Brown (1999) consider that yearling males delay sexual maturity in order not to pay any physiological costs of high testosterone levels. Furthermore, yearling males of the Mexican Jay may be tolerated by other males to a greater extent than those males with high testosterone levels, because they are readily identifiable through their juvenile bill coloration (Vleck & Brown 1999). The spotted-throat coloration of the male Rufous Vanga might have a similar effect as the bill coloration of the Mexican Jay, and is assumed to be an example of delayed plumage maturation (Rohwer et al. 1980; Greene et al. 2000). Delayed maturation is expected to delay the dispersal of males, and therefore may be closely related to the maintenance of the cooperative breeding system of

the Rufous Vanga. Additionally, it is evident that females achieve sexual maturity at age one, and thus the delayed maturation of males affects the operational sex ratio. Although the population sex ratio containing yearling males was biased toward males (0.60 on average), the operational sex ratio was 0.55 on average (Asai et al. unpubl.).

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ORIGINAL ARTICLE

Nest-site selection of the Red-billed Leiothrix and Japanese Bush Warbler in Japan

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Abstract The Red-billed Leiothrix *Leiothrix lutea* has been introduced from China and is rapidly increasing in deciduous broad-leaved forests of Japan. We studied nest-site characteristics and nest-site selection of this species and the Japanese Bush Warbler *Cettia diphone*, a sympatric native species, in southwestern Japan. Both species placed nests exclusively in bamboo thickets and on bamboo stalks. The Red-billed Leiothrix built pendulous nests in the canopy of high concealment. The Japanese Bush Warbler placed nests on the crossing of bamboo stems and selected places of high stem density. The Japanese Bush Warblers placed nests in denser vegetation than the Red-billed Leiothrix. The segregation of nesting microhabitat was also evident in both species to coexist in bamboo thickets. Existence of few inhabitants in bamboo thickets may contribute to the invasion success of the Red-billed Leiothrix.

Key words *Cettia diphone*, Introduced birds, *Leiothrix lutea*, Nest-site selection

Many birds have been transported out of their native ranges for trading, which has facilitated establishment of naturalised populations in various regions of the world (Long 1981). Biological invasion raises several ecological questions. First, what factors affect invasion success (Case 1991; Veltman et al. 1996). Second, what are the direct or indirect influences of introduced species on native species (Diamond & Case 1985; Lodge 1993). The second question is especially important for people who deal with the conservation of native avifaunas. In spite of its importance, there have been few studies on this subject, particularly during the establishment of introduced birds.

Introduced birds may diminish the number of native species through interspecific competition (Mountainspring & Scott 1985; Jones 1996). However, existence of interspecific competition is hard to detect (Lodge 1993), and evaluations of the influences of introduced birds on native ones have caused disputes (e.g. Moulton & Pimm 1983; 1986; Simberloff & Boecklen 1991; Simberloff 1992; Moulton 1993). It is important to clarify the ecological characteristics of

both introduced and native species in order to discern the reasons for successful introduction and competition between them. A study of habitat selection is one approach to achieve this clarification (Sol et al. 1997).

Of forest-living birds which are believed to be less successful in establishment (Long 1981), two timaliid species (Melodious Laughing-thrush *Garrulax canorus* and Red-billed Leiothrix *Leiothrix lutea*) and the Japanese White-eye *Zosterops japonica* have successfully established in native forests of Hawaii (Mountainspring & Scott 1985). The Red-billed Leiothrix has established also in deciduous broad-leaved forests of Japan in recent years (Yamashina Institute for Ornithology 1993; Eguchi & Masuda 1994). Notably, the same species have established in native forests of different regions which are believed to be resistant habitats to exotic birds.

The Red-billed Leiothrix ranged originally from southern China to the Himalayan region (Ali & Ripley 1972; Long 1987) and is a popular caged bird in Western countries. In Hawaii, North America and the European continent, naturalised populations have been reported (Long 1981; Lever 1987). In Japan, the number of naturalised individuals has been increasing rapidly in deciduous broad-leaved forests above

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1,000 m in elevation during the past two decades (Eguchi & Masuda 1994; Tojo 1994). However, information on the ecology of the Red-billed Leiothrix in natural habitat is generally lacking in native and introduced regions (but see Fisher & Baldwin 1947; Ralph et al. 1998).

In deciduous broad-leaved forests in Japan, the Red-billed Leiothrix forages in the lower layer of the forest and nests in thickets of dwarf bamboo (Eguchi & Masuda 1994). Only one sympatric species, the Japanese Bush Warbler *Cettia diphone*, nests in the same habitat where competition between them is likely. In Hawaiian islands, the Red-billed Leiothrix and Melodious Laughing-thrush diminished the number of native species through interspecific competition (Mountainspring & Scott 1985). Whether such an influence upon Japanese Bush Warblers has been exerted by the Red-billed Leiothrix is an important concern. Two major resources, nest-sites and foods, may be limiting, if competition exists. Our objective is to clarify characteristics and selection of nest-site in the two species and to determine the effect of nest-site microhabitat on nesting success. We discuss the possible impact of the Red-billed Leiothrix on native species with reference to the utilisation of nesting habitat.

METHODS

The study was conducted from April to August, 1997–1999 in the Ebino Plateau, Miyazaki and Kagoshima Prefectures, southwestern Japan (1,200 m elevation; 31°56'N, 130°51'E). The main study area was a mixed forest (16 ha) composed of *Abies firma*, *Tsuga sieboldii*, *Pinus densiflora*, *Quercus crispula*, *Hydrangea paniculata*, *Symplocos coreana* and *S. myrtacea*. In the shrub layer, dwarf bamboo *Sasamorpha borealis* of ca. 2 m in height, was spread predominantly throughout the forest, with small patches of bare ground. A road of ca. 10 m in width ran through the forest (Fig. 1). In 1997, additional data were collected at a 6 ha site, 800 m northwest of the main study area. The vegetational structure in the second site was the same as in the main study area. The annual mean precipitation exceeds 5,000 mm on the Ebino Plateau, of which more than one-third occurs during June and July (data from Miyazaki Branch, Weather Service of Japan). It was about twenty years since the Red-billed Leiothrix was first recorded in this area (Kamitanigawa pers. comm.).

Nests were located by systematic searches in the

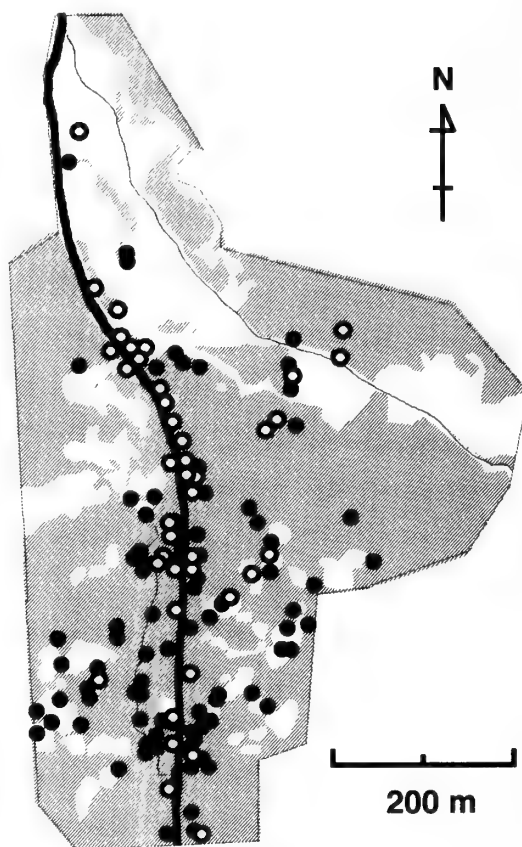


Fig. 1. Distribution of nests at a study site in 1998. Closed circles are the nests of Red-billed Leiothrix and open circles are those of Japanese Bush Warbler. The thick line is a road and thin lines are paths. All of the study area is covered with a continuous canopy of tall trees with dwarf bamboo (hatched areas) and bare ground (open areas) comprising the understorey.

bamboo thicket, using song and behaviour of birds as a cue. Nests were marked with plastic flags. Nests were checked at 3–7 days intervals until failure or fledging. Chicks of both species fledge between 10 to 15 days after hatching (pers. obs.). If chicks disappeared during this stage, we searched for them around nest-sites to confirm whether they fledged or not. If at least one chick fledged, the nest was assigned as “successful”. Because we could not distinguish between first and second nesting attempts for most nests, we combined them in the analyses.

After the termination of breeding, each nest was visited for measurement of nest-site characteristics. Variables measured were; size of nest, nest materials, nest height from the ground, height of bamboo canopy, length of the longest stalk supporting a nest, distance from the root of supporting bamboo to the nest, the number of twigs supporting a nest, the num-

ber of stems supporting a nest, distances from nearest stream, road, and edge of thicket, and density of vegetation. The density of vegetation was evaluated as follows. A red plastic board (25×40 cm) was placed 50 cm above the ground adjacent to the stalks supporting the nest, and a photograph of the board was taken from 1 m away. We scanned these photographs and measured the area of the red portion of the board using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/niimage/>) on a Macintosh computer. The density of vegetation is indicated by the area of the board obscured by the vegetation (=1,000—the area of red portion of the board). In 1999, we did not conduct nest measurements.

The density of the bamboo thicket varied from relatively open to quite dense. In order to examine the relationship between the density of bamboo and distance from the road, we sampled bamboo density in ten 50×50 cm quadrats (2 quadrats sets 2 m apart at 10 m intervals) along a 50 m transect. Five and four transects were set east and west of the road, respectively. We counted the number of live bamboo stems in each quadrat. Data from two quadrats were summed for each point. Similarly, four transects were set parallel to the road between neighbouring streams.

Because the foliage of bamboo is concentrated around the terminal end of the stem, nests in the foliage are of low visibility while those in the middle of stem are of high visibility. In 1999, in order to examine the nest-site selection of both species, the stem density and the visibility index were measured at the nests and at control points. To quantify the stem density, we counted the number of stems in a quadrat of 50×50 cm. Three visibility indices were measured as follows. A white board (30×45 cm) with 5×5 cm grids was placed at heights of 1 m (approximate bush warbler nest level) and 1.8 m (approximate leiothrix nest level). At a distance of 1.5 m from the board, we counted the number of intersections visible with the naked eye or through a video camera. The index ranged from 0 (no visibility) to 54 (perfect visibility). In order to quantify the degree of visibility at height of 1.8 m (the level of bamboo canopy), we used two different indices, the one from a point 1 m above the ground and the other from a point 1.8 m above the ground. Control points were chosen at a distance of 10 m north of each nest. If the point chosen fell on bare ground, another point was chosen to the south of

the nest.

Logistic regression analysis of data collected in 1999 was used to determine characteristics related to nest-site selection. The dependent variable was nominal: places preferred for nesting and control points. Independent variables were stem density and the three visibility indices.

Only completed nests were used for the analyses. Except for the interspecific comparison of the density of vegetation around nests and the analysis of nesting success, only data from the main study area were used. However, because all information was not always obtained for all nests, sample sizes were different among analyses. Means are shown with SD. A significant level is at $\alpha=0.05$.

RESULTS

1) Nest shape and nest attachment

Many more Red-billed Leiothrix' nests were found than those of the Japanese Bush Warbler: 67 nests (49 at the main site and 18 at the second site) in 1997, 83 in 1998, and 84 in 1999 for the Red-billed Leiothrix, compared to 25 nests (17 at the main site and 8 at the second site) in 1997, 41 in 1998, 22 in 1999 for the Japanese Bush Warbler. New nests of the Red-billed Leiothrix were cup-shaped, 9.7 ± 1.0 cm in diameter and 9.3 ± 1.2 cm in height for 135 nests measured (data combined for 1997 and 1998) and were made of blades of bamboo, moss, roots of plants and, sometimes, plastic cords. Nests of the Japanese Bush Warbler were elliptical ball-shaped, 10.1 ± 1.4 cm in diameter and 14.9 ± 2.4 cm in height for 56 nests measured, and were made entirely of blades of bamboo. Both species placed nests on bamboo stalks in dense bamboo thickets. Only one nest of the Red-billed Leiothrix was found in the understory lacking bamboo and dominated by *Symplocos myrtacea*.

The Red-billed Leiothrix placed their nests in foliage at the top of bamboo stalks. Although the length of stalks ranged from 2 to 3 m, stalks bent due to the weight of the nest so the nest height fell in the range of 1–2.5 m above the ground (Table 1). Nests were hung at the forks of stems with roots of plants and plastic cords. Each nest was supported by two or three stems. In a few cases, only one stem supporting the nest. The Japanese Bush Warbler placed nests at the middle height of stems, 0.5–2 m from the ground. Nests were attached to four or five stem crossings and were held to the stems rather than tied. Therefore, more stems were necessary to support a nest of the

Japanese Bush Warbler than that of the Red-billed Leiothrix (Table 1). The nest height of Japanese Bush Warblers was lower than that of the Red-billed Leiothrix, though not significant, in 1997. However, this does not mean that the Japanese Bush Warblers preferred short bamboo thickets. The height of vegetation around the nests was not significantly different between these two species (Table 1). The Japanese Bush Warbler preferred nesting lower on the bamboo stalks than the Red-billed Leiothrix.

A high density of stems were necessary for the Japanese Bush Warbler to fasten the nest, while density of stems was not so important for the Red-billed Leiothrix. Many nests of Japanese Bush Warblers were located where the density of vegetation was high (Fig. 2). Mean values of indices of vegetation density were 743.9 ± 107.0 ($N=68$) in 1997 and 529.9 ± 157.7 ($N=70$) in 1998 for the Red-billed Leiothrix, and 808.5 ± 116.3 ($N=26$) in 1997 and 604.8 ± 148.6 ($N=27$) in 1998 for the Japanese Bush Warbler. In both years, Japanese Bush Warblers placed nests in denser vegetation than Red-billed Leiothrix ($U_{26,68}=572$, $P=0.01$ in 1997, $U_{27,70}=698$, $P=0.05$ in 1998; Mann-Whitney U-test).

Overlap in the spatial distribution of nests between both species was large (Fig. 1). However, nests of the Red-billed Leiothrix were distributed throughout the study area while those of Japanese Bush Warblers

were concentrated near the road. The proportion of nests within 10 m of the road was greater for Japanese Bush Warblers than for Red-billed Leiothrix in both 1997 and 1998 (Table 2). Streams and bare ground also interrupted the bamboo thicket. The proportions of nests within 10 m of streams or bare ground were not different between the two species (Table 2).

The bamboo thicket was densest near the road (Fig. 3). However, there was not a consistent tendency between the density of bamboo stalks and the distance from a stream; 27.5 ± 15.0 stalks per 5,000 cm^2 ($N=13$) within 10 m of a stream and 22.6 ± 17.0 stalks ($N=13$) more than 10 m from a stream ($U_{13,13}=65.5$, $P>0.30$, Mann-Whitney U-test). Because tall trees were lacking near the road, the bamboo thicket grew well. However, because there was a continuous canopy of tall trees over the streams, the density of the bamboo thicket was not as high there, as near the road (27.5 ± 15.0 stalks ($N=13$), versus 95.6 ± 33.7 stalks ($N=9$), respectively, $U_{9,13}=0$, $P<0.0001$).

2) Nest-site selection

In the bamboo thickets, both species selected nest-sites non-randomly. Nests were placed at points of higher concealment and higher density of bamboo stems than control points by both species (Table 3).

Table 1. Comparison of nest placement between Red-billed Leiothrix and Japanese Bush Warbler.

		1997				1998							
		Red-billed Leiothrix		Japanese Bush Warbler		Red-billed Leiothrix		Japanese Bush Warbler					
		N											
		40		16		72		32					
		mean	SD	mean	SD	mean	SD	mean	SD	U	P ^e		
Height (cm)	Nest	165.8	34.7	146.9	27.3	232	>0.10	159.7	33.3	137.8	32.2	731.5	<0.01
	Bamboo	236.3	29.9	238.8	25.8	313	>0.80	218.8	41.5	220.9	34.8	1087	>0.60
Length (cm)	Nest ^a	—	—	—	—	—	—	214.4	38.5	142.2	37.6	219.5	<0.001
	Bamboo ^b	—	—	—	—	—	—	257.1	37.1	220.9	37.5	524.5	<0.001
Relative nest height ^c		3.8	0.5	3.0	0.6	112	<0.001	3.7	0.5	2.9	0.5	334	<0.001
Nest attachment ^d	Twig	6.3	2.3	6.1	1.6	314.5	>0.90	6.5	2.1	7.8	2.3	750.5	<0.01
	Stem	2.6	1.2	4.0	1.4	138	0.001	2.9	1.0	4.8	1.4	309.5	<0.001

^a distance from the root of supporting bamboo to the nest

^b length of the longest stalk supporting a nest

^c divided into four portions (1st, 2nd, 3rd and 4th from ground to top)

^d number of twigs (stems) supporting a nest

^e Mann-Whitney's U test

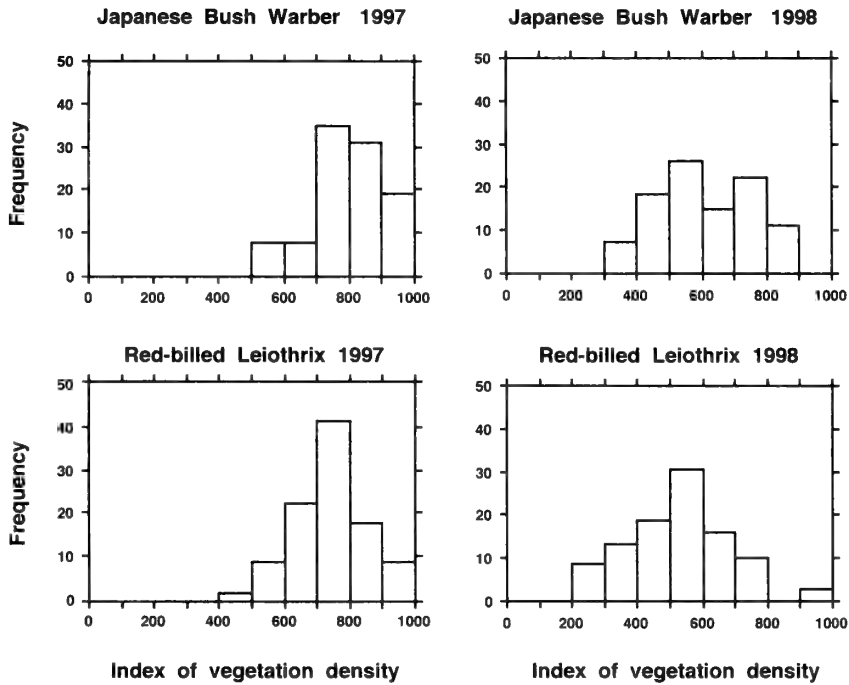


Fig. 2. Comparisons of the density of vegetation around nests between the Red-billed Leiothrix and the Japanese Bush Warbler. The index of vegetation density is shown as an area of a board covered with vegetation.

Table 2. Locations of nests of Red-billed Leiothrix and Japanese Bush Warbler.

		1997		1998	
		Red-billed Leiothrix	Japanese Bush Warbler	Red-billed Leiothrix	Japanese Bush Warbler
N		50	18	77	36
Distance from road	Less than 10 m	6	10	21	26
	More than 10 m	44	8	56	10
	p^a		0.001		<0.001
Distance from bare ground	Less than 10 m	24	7	30	11
	More than 10 m	26	11	47	25
	p^a		>0.50		>0.40
Distance from streams	Less than 10 m	22	5	46	24
	More than 10 m	28	13	31	12
	p^a		>0.20		>0.50

^a Fisher's exact probability-test

For Red-billed Leiothrix, the differences were significant for the stem density and visibility indices in the canopy but not for the visibility index at the lower height. However, logistic regression indicated that the overall contribution of these variables was low ($R^2=0.14$) and no particular characteristic was re-

lated to the separation between nests and control points (Table 4). On the other hand, the Japanese Bush Warbler selected high stem density and well concealed places. The density of bamboo stems and visibility index in the canopy were related to the separation between nests and control points (Table 4).

3) Nesting success and vegetation density at nest-site

In the Red-billed Leiothrix, fate of 51 nests was traced and five nests were successful (9.8%) in 1997, five from 63 nests (7.9%) in 1998, and only two from

68 nests (2.9%) in 1999, respectively. In the Japanese Bush Warbler, only one nest was successful from 18 nests (5.3%) in 1997, and no nest was successful in both 1998 (from 33 nests) and 1999 (from 14 nests). More than a half of nests studied were left no egg laid. In the Red-billed Leiothrix, the proportions of nests in which eggs were laid were 43.1% (=22/51), 34.9% (=22/63), 39.7% (=27/68), in 1997, 1998 and 1999, respectively. In the Japanese Bush Warbler, the proportions of nests in which eggs were laid were 50.0% (=9/18), 36.4% (=12/33), 21.4% (=3/14), in 1997, 1998 and 1999, respectively. We could not determine whether these failed nests were deserted before clutch initiation or were depredated soon after that. Most failures after clutch initiation were due to total loss of clutches or broods, which suggests nest predation. Combined data for three years: 58 of 59 nests in which causes of failure were confirmed in the Red-billed Leiothrix and 20 of 23 nests in the Japanese Bush Warbler. We observed the Jay *Garrulus glandarius* and snakes (species unknown) predating nestlings.

In the Red-billed Leiothrix, neither the density of vegetation nor nest height related to nesting success. The indices of vegetation density of the successful nests and failed nests were 769.9 ± 166.8 vs. 740.8 ± 101.9 in 1997 ($U_{5,42}=83$, $P>0.40$; Mann-Whitney U-test), 586.3 ± 224.2 vs. 528.8 ± 147.3 in 1998 ($U_{5,49}=90$, $P>0.30$) and the nest height were 174.0 ± 48.3 cm

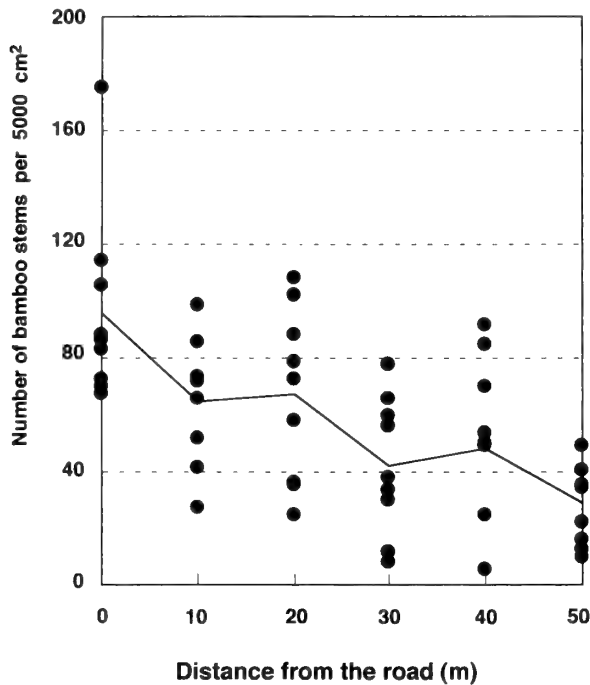


Fig. 3. The relationship between the density of bamboo stems and distance from the road. The line connects means.

Table 3. Comparison of the stem density and the visibility index between nests and control points for Red-billed Leiothrix and Japanese Bush Warbler.

		Red-billed Leiothrix		Japanese Bush Warbler	
		N	31	22	
			mean	mean	SD
No. of stems	Nest		27.6	38.3	11.4
	control		19.7	23.1	11.5
	P^a		<0.05	0.001	
Visibility index 1 m above ground	Nest		16.4	13.3	7.6
	control		21.5	18.4	10.0
	P^a		>0.10	<0.05	
canopy from below	Nest		5.4	5.6	6.9
	control		9.6	8.0	6.6
	P^a		<0.05	<0.05	
canopy level	Nest		4.4	3.1	3.3
	control		8.8	8.2	8.0
	P^a		<0.01	0.001	

^a Wilcoxon's signed-ranks test

Table 4. Logistic regression analysis of the stem density and the visibility index between nests and control points for Red-billed Leiothrix and Japanese Bush Warbler.

N Characteristics	Red-billed Leiothrix		Japanese Bush Warbler	
	Parameter estimate	P	Parameter estimate	P
Intersect	-0.77	0.53	2.64	0.15
Density of stems	-0.02	0.48	-0.11	0.01
Visibility index at 1 m above ground	0.01	0.72	0.01	0.93
Visibility index in canopy from below	0.08	0.29	-0.13	0.14
Visibility index in canopy	0.07	0.29	0.27	0.04
	$R^2=0.14$		$R^2=0.36$	

vs. 162.9 ± 32.5 cm ($U_{5,42}=90$, $P>0.60$ in 1997), 152.0 ± 32.7 cm vs. 156.1 ± 31.3 cm in 1998 ($U_{5,49}=98$, $P>0.40$; Mann-Whitney U-test). In the Japanese Bush Warbler, sample sizes of nesting success were too small to test.

In 1999, because few nests were successful, we could not show the relationships between nesting success and nest characteristics (the stem density and indices of visibility).

DISCUSSION

1) Utilisation of bamboo thickets

The Red-billed Leiothrix builds nests on bamboo not only in the Ebino Plateau but also in other areas of Japan (this study; Nakamura & Tojo unpubl.; Eguchi & Amano unpubl.). Only a few species are known to nest in bamboo thickets in Japan, including the Japanese Bush Warbler, Grey Bunting *Emberiza variabilis*, Siberian Meadow Bunting *E. cioides*, Bull-headed Shrike *Lanius bucephalus* and the Japanese White-eye (Kiyosu 1951). In Mt. Tsukuba, Ibaraki prefecture, the Japanese Bush Warbler, Japanese White-eye, Siberian Meadow Bunting and Long-tailed Tit *Aegithalos caudatus* nest in thickets of bamboo *Sasamorphia borealis* (Nakamura & Tojo unpubl.). On the Kayanodaira Plateau, Nagano Prefecture, the Japanese Bush Warbler and Grey Bunting are the dominate nesting species in thickets of dwarf bamboo *Sasa senanensis* and *S. kurilensis* (Ezaki pers. comm.). However, only two native species, the Japanese Bush Warbler and Grey Bunting, nest predominantly in bamboo thickets in Japan. Although the avifauna is rich in deciduous broad-leaved forests, it is likely that the microhabitat which the Red-billed Leiothrix uses for nesting has been vacant.

The Red-billed Leiothrix is not a specialist nesting on bamboo stalks in its original habitats (Ali & Ripley 1972; Long 1987). In Hawaii, Red-billed Leiothrix nests in dense undergrowth, but does not specialise in a particular substrate tree species (Fisher & Baldwin 1947). Also in Japan, there have been a few cases where Red-billed Leiothrix nested on shrub trees, such as *Symplocos myrtacea*, *Abies firma*, *Eurya japonica*, *Litsea glauca*, and *Camellia japonica* (Eguchi & Amano unpubl.). The Monk Parakeet *Myiopsitta monachus*, a habitat generalist in its original range, became a specialist nesting solely on palms of *Phoenix* sp. in Spain (Sol et al. 1997). Sol et al. (1997) suggested that the preference of a habitat occupied by no other species allows the parakeet to increase rapidly in the initial stage of invasion and that gradually it expands the width of habitat preference after successful establishment. The Red-billed Leiothrix also could increase in number by nesting in bamboo thickets where few competitors live and by specializing in nesting substrate and position of the nest.

2) Difference in nest-site selection

Both the Red-billed Leiothrix and Japanese Bush Warbler selected dense vegetation for nesting. However, the species selected different nesting microhabitats. Red-billed Leiothrix built nests in the canopy of bamboos, while the Japanese Bush Warbler placed nests at the middle height of stems. Such a difference may be due primarily to a difference in manner of nest attachment between two species.

The Red-billed Leiothrix built pendulous nests at the top of bamboo stalks, while Japanese Bush Warblers built nests at the crossing of bamboo stems. Japanese Bush Warblers require a bamboo thicket of

high density for fastening nests firmly. Therefore, nests of Japanese Bush Warblers are distributed in the vicinity of the forest edge, such as near roads where the bamboo thicket is densest. On the other hand, because the density of bamboo stalks is not important for attaching nests, the Red-billed Leiothrix selects a wider range of understory density for nest-sites than the Japanese Bush Warbler.

The Japanese Bush Warbler also places nests in the middle of the bamboo stem in other regions of Japan. On the Kayanodaira Plateau where the Red-billed Leiothrix has not invaded yet, the Grey Bunting places nests at the top of bamboo stalks in areas of relatively sparse thickets, while the Japanese Bush Warbler nests in denser thickets (Ezaki pers. comm.). Thus, two species with different nest-site preferences could coexist in bamboo thickets.

3) Nest-site selection and nesting success

Dense vegetation may provide shrub-nesting species excellent protection against predators and non-random nest-site selection has been found in other such species (e.g. Black-throated Blue Warbler, Holway 1991; Hooded Warbler, Kilgo et al. 1996; Wood Thrush, Hoover & Brittingham 1998). The Japanese Bush Warbler selected places of high stem density. Dense bamboo stalks may impede the movement of predators. The Red-billed Leiothrix placed nests in the canopy of bamboos of high concealment. However, logistic regression suggested that this species may not always select a place of highest concealment in a territory for nesting. The Red-billed Leiothrix sometimes built an exposed nest just above a stream. Apparently, nest concealment is not a primary factor determining nest-site selection in this species.

Although the Red-billed Leiothrix and Japanese Bush Warbler selected somewhat of nest-site characteristics, the nesting success was very low in these species due to predation, particularly evident in almost all nests of the Japanese Bush Warbler. The density of vegetation at the nest site and nest height did not influence nesting success. We observed nest predation by the Jay and snakes (species unknown). Another potential predator may be the Jungle Crow *Corvus macrorhynchos*. Avian predators such as corvids depend on visual cues, and activities of parent birds may be important cues for such predators (Holway 1991; Hoover & Brittingham 1998). We often observed jays flushing from canopies of bamboos. Some jays may have searched exclusively for

nests of birds nesting in the bamboo thicket when eggs and nestlings of these species were available. On the other hand, snakes search for nests using olfactory cues (Burhans & Thompson 1998). The effect of nest-site characteristics to predation may vary depending on the predator species. If a guild of predators is composed of species searching in different ways, selection of a specific type of nest-site may not be advantageous (Filliater et al. 1994; Hoover & Brittingham 1998). High nest predation and failure to detect a significant relationship between nesting success and nest characters in this study may be due to a varied predator community.

Moreover, because the Red-billed Leiothrix is a newcomer in this area, there may have not been enough time for a counter adaptation against a new guild of predators to appear. However, this species re-nested rapidly after predation and breeding season was long, with egg-laying occurring from April to September (pers. obs.). Rapid re-nesting and a long breeding season may be adaptations to high nest predation as reported in other shrub-nesting species (Martin 1995). Further studies evaluating a role of each taxonomic group of predators on mortality of birds nesting in the bamboo thicket are needed.

4) Influence on breeding of the Japanese Bush Warbler

So far, no distinct influence of the Red-billed Leiothrix on native species, such as a decline in number or habitat shrinkage, has yet been reported. The locations of nests in the bamboo thicket differ between the Red-billed Leiothrix and Japanese Bush Warbler. Even in the case where nests of these species were close to each other, direct interaction suggesting interspecific territoriality was not observed. It is unlikely that competition for nest-sites occurs between these species.

However, indirect interference competition is probable. In the community of *Acrocephalus* warblers in the reed beds of Europe, such an increase of predation due to the coexistence of species of similar nest-site preference is also considered probable (Hoi et al. 1991).

When we searched for nests of the Red-billed Leiothrix, nests of the Japanese Bush Warbler were also found. A high density of nests may attract various kinds of predators into the breeding areas. In this study, the density of Red-billed Leiothrix nests, which was two to three times higher than that of Japanese Bush Warblers, may have caused an in-

crease in the number of predators and predation on nests of shrub-living species (the functional response; Holling 1959). The breeding success of Japanese Bush Warbler may be low due to indirect interference competition caused by the increase of Red-billed Leiothrix. Further studies are needed including a monitoring in an area of initial invasion or eliminating experiments for the Red-billed Leiothrix.

The Red-billed Leiothrix has invaded various regions of the world (Long 1981). Comparisons of habitat selection among naturalised populations and among naturalised populations and populations in their original range may indicate flexibility of habitat preference in this species, as well as changes in habitat selection during the process of invasion. Further studies are needed both in the original and new habitats of the Red-billed Leiothrix.

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ORNITHOLOGICAL SCIENCE

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Contents

PREFACE

Higuchi H

From Japan through Asia to the world:
building bridges in ornithological science. 1

EDITORIAL

Ueda K

"Ornithological Science", the new English
publication from Japan. 3

SPECIAL FEATURE

Interspecific segregation and attraction in forest birds

Hino T

Introduction. 5

Loyn RH

Patterns of ecological segregation among
forest and woodland birds in south-eastern
Australia. 7

Recher HF, Davis WE Jr & Calver MC

Comparative foraging ecology of five
species of ground-pouncing birds in western
Australian woodlands with comments on
species decline. 29

Mönkkönen M & Forsman JT

Heterospecific attraction among forest birds:
a review. 41

Seki S & Sato T

The effect of a typhoon on the flocking and
foraging behavior of tits. 53

Murakami M

Foraging mode shifts of four insectivorous
bird species under temporally varying
resource distribution in a Japanese
deciduous forest. 63

Mizutani M & Hijii N

The effects of arthropod abundance and size
on the nestling diet of two *Parus* species. 71

Hino T, Unno A & Nakano S

Prey distribution and foraging preference for
tits. 81

Sodhi NS

The effects of food-supply on Southeast
Asian forest birds. 89

ORIGINAL ARTICLES

Yamagishi S, Asai S, Eguchi K & Wada M

Spotted-throat individuals of the Rufous
Vanga *Schetba rufa* are yearling males and
presumably sterile. 95

Amano HE & Eguchi K

Nest-site selection of the Red-billed
Leiothrix and Japanese Bush Warbler in
Japan. 101

08 JAN 2003

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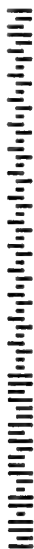
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ORIGINAL ARTICLE

Breeding bird community and mixed-species flocking in a deciduous broad-leaved forest in western Madagascar

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Abstract The breeding bird population of a deciduous broadleaved forest in western Madagascar was censused by means of territory mapping. Despite the foliage structure being simpler, neither species richness nor density was less than those in mature temperate forests. Species diversity was higher in the western Madagascan forest owing to the higher species evenness. Tree-cavity nesters and bark foragers were few because woodpeckers, nuthatches, and tits have not colonized Madagascar. The scarcity of birds nesting on or near the forest floor may be attributable to abundance of nest-predators such as large lizards and snakes in these areas. The bird community was dominated in abundance by the members of mixed-species flocks, almost all of which forage in the canopy. Mixed-flocking can be beneficial for these birds to avoid predation by raptors, which were frequently observed in the canopy. Since most of the flock members had relatively similar territory sizes resulting in similar densities, the high species evenness in this community may have resulted from mixed-flocking by canopy-foraging species.

Key words Forest bird community, Madagascar, Mixed-species flocks, Predators, Species evenness

Bird species diversity is generally higher in tropical forests than in temperate forests. This latitudinal gradient of species diversity has been mainly explained by external factors such as the structural complexity of habitat (MacArthur et al. 1966), climatic stability (Stiles 1978) and predictability or diversity of food resources (Karr 1971; Schoener 1971). In contrast, Powell (1989) explained the high species richness in the neotropical avifauna as arising from the internal structure of the community itself. Multispecies territoriality (i.e., the year-round communal defence of territory) by the core species of mixed-species flocks reduces the densities of small species because they have larger territories than expected from their body size. As a result, a greater number of small species can coexist owing to the under-utilization of food resources in such a community.

Madagascar, which lies within the tropical region, supports various kinds of forests including: rain forest, deciduous broad-leaved forest, and subarid scrub.

Although the avifauna is highly unique with >50% of the breeding species endemic (Langrand 1990), there have been no quantitative studies of Madagascan forest bird communities. Multispecies bird flocks are observed all year round in Madagascan forests (Eguchi et al. 1993; Hino 1998, 2000) as well as in other tropical forests (Bell 1983; Powell 1989; Jullien & Thiollay 1998). Hino (1998, 2000) has shown that the core species of mixed flocks in deciduous broadleaved forest in Madagascar gain mutual benefits relating to foraging and/or anti-predation. The deciduous forest is an appropriate habitat to examine the factors, other than foliage structure, that may explain the differences between bird communities in tropical and temperate forests. In this paper, I describe the characteristics of breeding bird communities in a deciduous broad-leaved forest in western Madagascar by comparing them with those of temperate forests in Japan. Then I consider the effect of predators and multispecies flocking to explain the characteristics of the Madagascan bird community.

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METHODS

This study was conducted in a 450×550-m quadrat (called Jardin A) in a deciduous broadleaved forest in the Ampijoroa Forest Reserve (16°35'S, 46°82'E; ca. 200 m asl), about 110 km southeast of Mahajanga. In this forest, 113 tree species are listed by Razafy (1987). The mean annual precipitation of the area is about 1500 mm, 97% of which is recorded during the wet season (November to April), and the mean annual temperature is 26.8°C (Razafy 1987).

Ten censuses of breeding bird populations were conducted using the territory mapping method, walking steadily around the whole study site from 10–20 October 1994. All birds seen or heard within 50 m of either side of the census trail were recorded on a scale map. The territories overlapping the border of the study area were recorded as half territories (0.5). Raptorial species (e.g. *Otus rutilus*, *Accipiter madagascariensis*, *A. francessi*, *Polyboroides radiatus*) and forest-edge species (e.g. *Falco p. palliata*, *Merops superciliosus*, *Caprimulgus madagascariensis*, *Coracopsis vasa*), which were observed during the census, were excluded from the analysis of this study.

At each encounter, whether each individual participated in mixed-species flocks (foraging with two or more different species for more than 10 min; Jullien & Thiollay 1998) was recorded from 10 October to 12 November. The mixed-flocking propensity of each species was calculated as the percentage of the number of times the species was found foraging in a mixed flock relative to the total number of times this species was encountered (Jullien & Thiollay 1998). Categorization of foraging and nesting habits followed Langrand (1990), Yamagishi et al. (1997), Morris and Hawkins (1998) and my field observations, and body lengths followed Langrand (1990). Species diversity (D) and evenness (E) were calculated using Simpson's indices: $D = 1/\sum P_i^2$ and $E = D/S$, where P_i is the proportion of abundance for species i and S is the number of species.

Vegetation structure was surveyed in 120 sample plots (5 m×5 m) at 50 m intervals on 15–17 November 1994. The number of trees or woody plants stems in each of four categories of diameter at breast height (DBH: <5 cm, 5–15 cm, 15–30 cm, 30 cm<) and the height of the tallest tree were recorded for each plot. At eight different height strata (0–1 m, 1–2 m, 2–4 m, 4–6 m, 6–10 m, 10 m<), and four categories of foliage volume (0: none, 1: 1–33%, 2: 34–66%, 3: 67–

100%) were recorded by eye in all plots, averaged and multiplied by 25% for each stratum.

For comparison, three studies of the bird communities in deciduous broadleaved forests in Japan were selected. The following points were considered in selecting the studies: (1) the territory mapping technique had been used; (2) the number of censuses was equal to or greater than 10; (3) the census area was larger than 10 ha; (4) the forests were natural and undisturbed (e.g. no grazing); (5) coniferous trees were not a major component of the forests; (6) the forest area, including the census site, was large enough not to be influenced by surrounding habitats.

RESULTS

The Madagascan study site was characterized by its high density of small trees or woody plants <15 cm in DBH (Table 1). The canopy was lower than 16 m (mean=12.4 m±1.3 SD, N=120). Foliage coverage was most dense at 4–8 m in height (Fig. 1).

Table 1. Densities of trees and woody plants in DBH-class.

DBH (cm)	Number/ha
1–5	23,294
5–15	3,455
15–30	336
30–	54
Total	27,139

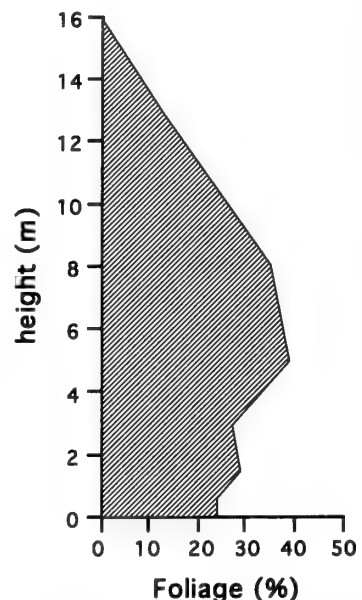


Fig. 1. Vertical distribution of foliage coverage.

Table 2. The body length, nesting- and foraging-sites, food item, density and mixed-flocking propensity of each species of breeding birds.

Species	BL ¹ (cm)	Nesting site ²	Foraging site ³	Food item ⁴	Density (pairs/km ²)	Mixed-flocking propensity (%) ⁵
<i>Dicrurus forficatus</i>	26	C	F/A	A	28.3	48.1 (52)
<i>Schetba rufa</i>	20	C	G	A	34.3	50.0 (46)
<i>Cyanolanius madagascariensis</i>	16	C	F	A	20.2	87.5 (16)
<i>Xenopirostris damii</i>	23	C	B	A	4.0	36.4 (11)
<i>Leptopterus viridis</i>	20	C	B	A	2.0	33.3 (3)
<i>Nectarinia souimanga</i>	10–11	C	F	A/P	44.4	28.6 (21)
<i>Nectarinia notata</i>	14	C	F	A/P	12.1	25.0 (8)
<i>Terpsiphone mutata</i>	18	C	A	A	38.4	48.3 (58)
<i>Neomixis tenella</i>	10	C	F	A	34.3	35.7 (14)
<i>Newtonia brunneicauda</i>	12	C	F	A	58.6	56.3 (32)
<i>Copsychus albospecularis</i>	18	H	G	A	26.3	12.5 (16)
<i>Hypsipetes madagascariensis</i>	24	C	F	A/P	34.3	33.3 (18)
<i>Phyllastrephus madagascariensis</i>	18–22	C	F/B	A	28.3	76.0 (25)
<i>Coracina cinerea</i>	24	C	F	A	22.2	62.1 (29)
<i>Upupa epops</i>	32	H	G	A	10.1	14.3 (14)
<i>Leptosomus discolor</i>	50	H	F	A	4.0	0.0 (7)
<i>Eurystomus glaucurus</i>	29–32	H	F	A	6.1	0.0 (11)
<i>Centropus toulou</i>	45–50	C	G	A	4.0	0.0 (3)
<i>Coua cristata</i>	40–44	C	F	A	22.2	37.0 (27)
<i>Coua coquereli</i>	42	C	G	A	16.2	0.0 (21)
<i>Coua ruficeps</i>	42	C	G	A	12.1	0.0 (13)
<i>Cuculus rochii</i>	28	P	F	A	2.0	0.0 (3)
<i>Coracopsis nigra</i>	35	H	F	P	2.0	0.0 (4)
<i>Agapornis cana</i>	14–16	H	F	P	2.0	0.0 (3)
<i>Streptopelia picurata</i>	28	C	G	P	16.2	0.0 (17)
<i>Treron australis</i>	32	C	F	P	2.0	0.0 (2)
<i>Turnix nigricollis</i>	15	G	G	A/P	4.0	0.0 (5)
<i>Mesitornis variegata</i>	31	G	G	A/P	8.1	16.7 (6)
<i>Lophotibis cristata</i>	50	C	G	A	2.0	0.0 (6)

¹ Body length followed Langrand (1990).² C=canopy, H=tree-hole, G=ground or bush, D=deposition.³ F=foliage, B=bark, G=ground or bush, A=air, F/A or F/B=both sites.⁴ A=animals (arthropods, small reptiles), P=plant materials (seeds, fruits, nectar), A/P=both food.⁵ the percentage of the number of times found foraging in a mixed flock relative to the total number of times encountered (shown in parenthesis).

A total of 29 species and 499 pairs/km² of birds bred in the study area (Table 2). These values did not differ from those in Japanese forests (Table 3). Nevertheless, the species diversity was high in Madagascar owing to the high species evenness in comparison to Japanese communities (Table 3).

Most Madagascan birds (69% of species and 87% of individuals) nest in canopy foliage including tree forks, very few nest in tree-holes or on the ground (or in bushes) (Table 3). These nesting habits are very different from those of forest birds in Japan. The composition of foraging-site groups also differed be-

tween bird communities in Madagascar and Japan although the difference was very small in comparison to that of nesting-site groups. In Madagascar, bark-foraging birds were fewer while foliage-foraging birds were more abundant. The composition of the food items taken by both bird communities was similar.

Seventeen species were observed in mixed-species flocks during the breeding season. Of these, seven species were regular members of mixed flocks (flocking propensity=48–88%) and another seven species were occasional members (flocking propensity=25–

Table 3. A comparison of species numbers and densities of each group for nesting- and foraging sites and food items, species-diversity and evenness of the bird community between Madagascar and Japanese forest bird communities.

	Madagascar		Japan ⁵	
	No. of species ⁴	No. of pairs/km ²	No. of species ⁴	No. of pairs/km ²
Nesting site ¹				
C	20.0	436.4	7–11	61–83
T	6.0	50.5	10–12	195–279
U	2.0	12.1	7–9	111–209
D	1.0	2.0	1	2–9
Foraging site ²				
F	15.0	294.9	10–12	185–229
B	2.5	20.2	5–6	53–61
G	10.0	133.3	9–11	109–180
A	1.5	52.1	2–4	39–100
Food item ³				
A	22.5	427.3	20–21	317–404
P	6.5	73.7	7–9	74–152
O	0.0	0.0	1–2	2–6
Total	29.0	499.0	29–31	422–491
Species diversity		16.9		13.3–15.0
Species evenness		0.58		0.46–0.52

¹ C=canopy, H=tree-hole, G=ground or bush, D=deposition

² F=foliage, B=bark, G=ground or bush, A=air

³ A=animals (arthropods, small reptiles), P=plant materials (seeds, fruits, nectar), O=omnivorous food

⁴ 0.5 was given to each group for the birds categorized to two groups (e.g., F/B in Table 2)

⁵ Fujimaki (1986, 1988) and Hino & Nakano (1992).

37%). Almost all of these species were small- or medium sized birds (<30 cm in BL) eating arthropods or small reptiles in the canopy, although the substrates preferred (foliage, bark, air) varied among species. In contrast, the bird species that did not, or rarely participated in mixed flocks (flocking propensity=0–17%) were large birds (>30 cm) that typically forage on the ground and those that eat plant material.

Almost all of the most abundant species were regular or occasional members of mixed-species flocks (Fig. 2). A significant positive correlation was found between abundance and flocking propensity (Kendall's $\tau=0.506$, $P<0.0001$).

DISCUSSION

Although the deciduous broad-leaved forest studied in western Madagascar was mature, the characteristics of its vegetation structure (i.e. abundant small trees and low foliage height) corresponded to those of a young forest in a temperate region (Aber 1979). In

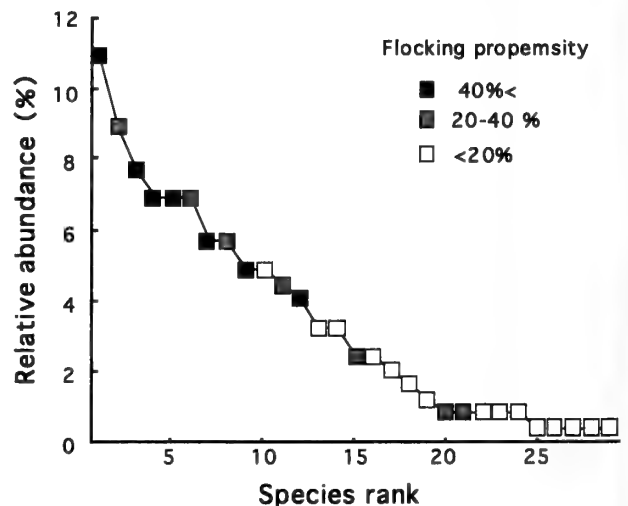


Fig. 2. Mixed-flocking propensity and the relative abundance of species arranged in decreasing order of abundance.

general, bird species diversities are lower in young forests than in mature forests owing to their simpler structure (Bongiorno 1982; Helle 1985).

Neither the species richness nor the density of breeding birds (except raptorial or forest-edge species) in the study area differed from those of mature temperate forests in Europe and Japan (about 30 species and 500–700 pairs/km²; Hino 1990, 1993). Moreover, species diversity was high owing to the high species evenness. That is, the Madagascan study area had a more diverse bird community than would be predicted from an examination of its vegetation structure. Razafy (1987) listed 113 species of trees in the forest reserve including the study area. This number of tree species is much higher than that seen in temperate forests (<40 species at most, Hino 1990). One of the factors explaining the high bird diversity of the study area may be the high tree species diversity of the forest. Many studies have shown that more diverse bird communities are found in forests with more diverse tree composition (e.g. Rice et al. 1984; Verner & Larson 1989).

The composition of nesting-site groups differed considerably between Madagascan and Japanese bird communities. Tree-hole nesters were few in Madagascar because ancestral woodpecker, nuthatch, and tit species failed to colonize the island. In particular, the absence of woodpeckers (which excavate their own nesting cavities annually thereby creating a valuable cavity resource in trees), must have had a considerable negative influence on the nesting habits of other species. The scarcity of species nesting on or near the forest floor may be attributable to the abundance of terrestrial nest-predators such as large lizards *Oplurus cuvieri* and snakes *Leioheterodon madagascariensis*. These reptiles are considered to be major predators on the eggs and/or fledgling of *Schetba rufa* (Eguchi et al. 2001), *Terpsiphone mutata* (T. Mizuta pers. com.) and *Coua coquereli* (T. Masuda pers. com.) although they build their nests in the low (1–5 m high) canopy.

The composition of foraging-site groups also differed in abundance between Madagascan and Japanese bird communities. The reason why the bark-foraging birds were few will be the same one why the cavity nesters are few, that is, the failure in colonization of ancestral woodpecker, nuthatch, and tit species. Although some of the Vangidae species observed during this study, such as *Xenopirostris damii* and *Leptopterus viridis*, have evolved as bark foragers thorough adaptive radiation (Yamagishi & Eguchi 1996), this niche seems not to have been full occupied by birds in Madagascar.

The present bird community was dominated, in

terms of abundance, by the members of mixed-species flocks. Flocking propensities were more than 48% among regularly flocking species and more than 25% among occasionally flocking species despite observations being made during the breeding season. In the non-breeding season, flocking propensities were almost double (Hino 1998). Almost all flocking species forage in the canopy, where raptors (e.g. *O. rutilus*, *A. madagascariensis*, *A. francessi*, *P. radiatus*) were frequently observed. Mixed-species flocking may be an effective strategy for avoiding predation as well as of achieving increased foraging efficiency (reviews in Morse 1977, Barnard and Thompson 1985). In fact, mobbing of raptors by flock members was often observed in the study area.

The anti-predatory value of mixed-flocking may be enhanced if the flock members move consistently together within a communal territory, that is, multi-species territoriality in neotropical rain forests (Munn & Terborgh 1979; Powell 1989; Jullien & Thiollay 1998). Powell (1989) demonstrated that multispecies territoriality should increase species richness. Species evenness should also increase through this system since the community is composed of species with the same density. Although the mixed-flock members in the study area did not hold communal territories rigorously, similar sized territories appear to be maintained by regular flock-members (except the most dominant species *Newtonia brunneicauda*) resulting in similar densities (20–38 pairs/km²). *N. brunneicauda* may have adjusted its home range size to that of the other flock members by forming conspecific flocks consisting of two pairs with neighboring territories (Hino 2000). In the present avian community, therefore, the high species evenness may have resulted from mixed-flocking among canopy-foraging species.

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ORIGINAL ARTICLE

Secondary users of Great Spotted Woodpecker (*Dendrocopos major*) nest cavities in urban and suburban forests in Sapporo City, northern Japan

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ORNITHOLOGICAL SCIENCE

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Abstract Old nest cavities excavated by Great Spotted Woodpeckers (GSW) *Dendrocopos major* were examined in two study areas (urban and suburban forests) in Sapporo, the capital city of Hokkaido, northern Japan. Five avian and one mammalian secondary cavity user (SCU) species occupied 47 of 101 GSW cavities inspected. The species composition differed between urban and suburban forests. Avian SCU species occupied GSW cavities more frequently in the urban than in the suburban forests. Tree Sparrows *Passer montanus* and Chestnut-cheeked Starlings *Sturnus philippensis* were the only dominant cavity breeding species in the severely fragmented urban forests. Flying Squirrels *Pteromys volans* were the most dominant users of GSW cavities in the suburban forests. The density of GSW cavities depends not only on natural processes but also on human activities. The suitability of the GSW cavities for certain SCU species decreases with time. To maintain the diversity of cavity-nesting wildlife in urban and suburban areas of Sapporo, preservation of existing trees with GSW cavities as well as providing suitable habitat conditions to support continued production of new cavities is essential.

Key words *Dendrocopos major*, Nest webs, Sapporo City, Secondary cavity user, Urban area

Cavity-nesting species comprise a major component of the forest wildlife community (Scott et al. 1980). Martin and Eadie (1999) proposed as a direct analogy to 'food webs' that cavity-nesting bird communities are organized in 'nest webs' with the cavities as the central resource, around which inter-specific and intra-specific interactions occur. In such a web structure, a certain species may have disproportionate importance if it constitutes a key component of the cavity resources. Primary cavity nesters (PCNs, e.g. woodpeckers) are such key components that excavate cavities used as nests or roosts by secondary cavity users (SCUs) including not only bird but also many other wildlife species. The SCUs rely on the cavities created by PCNs or on natural holes formed through other processes. The number of

available nesting cavities has been considered to be a major factor limiting the population size of SCU bird species (Haartman 1957; Perrins 1979; Newton 1994). Thus, the density and diversity of woodpeckers may have a strong influence on the richness and abundance of other SCU species (Martin & Eadie, 1999).

In recent years in Hokkaido, northern Japan, GSW is the only PCN species regularly breeding in urban areas (Yamauchi et al. 1997). In fact, GSW is now the most abundant and often the only PCN species in the urban area of Sapporo, the capital city of Hokkaido (Kotaka & Kameyama in press). In urban areas, GSW may affect entire communities of cavity-nesters through the excavation of nest cavities. However, information on the importance of GSW cavities for other species so far has been just anecdotal, and few studies have quantified utilization of GSW cavities by SCU species in urban areas of modern large cities such as Sapporo. The composition of the nest webs

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may also vary with habitat features such as forest type or landscape pattern.

In this paper, we compare the availability of GSW cavities and their actual occupation frequency by SCU species in two different types of forest (urban and suburban area) in Sapporo to develop a better understanding of the ecological role of GSWs within the nest webs.

STUDY AREAS AND METHODS

The GSW nest cavities were surveyed in two different types of landscapes in Sapporo; a highly fragmented forest in an urban area (HKD) and a less fragmented forest in an agricultural suburban area (HJO). Both areas are characterized by a relatively flat topography. The former (HKD) includes the University of Hokkaido Campus and its Botanical Garden located in the center of Sapporo (43°04'N, 141°20'E) and totalling 271 ha. This area is characterized by highly fragmented woodland (21.3% of tree coverage) comprising woodland with dense undergrowth, open woodland with little undergrowth, hedgerows, farmland, sports grounds, lawns and buildings. Dominant tree-species are *Acer mono* and *Ulmus japonica*. The latter (HJO) is situated in the grounds of the Hokkaido National Agricultural Experiment Station and the Forestry and Forest Products Research Institute, totalling about 380 ha, located in the southeastern part of Sapporo about 8 km from HKD. This area is characterized by farmland used mainly for crop production and grazing. The tree coverage is about 39.8%, and dominant tree species are *Quercus mongolica* and *Acer mono*.

Both study sites were searched for all new GSW nests (HKD in 1994–1997 and HJO in 1995–1998). Locations of the nest cavity-trees were mapped, and each tree was classified as living or dead. The GSW cavities were revisited and examined at least twice in late May and June during the period 1995–1998 in HKD and in 1999 in HJO. Use of the cavities was examined by climbing the trees to inspect cavities with a dentist's mirror. If adults, eggs or young of certain species were found, the cavity was classified as 'occupied'. The users of those cavities were identified through observation with binoculars. The nest cavities inspected were further classified into two categories according to their age, "1 year-old" if they were examined one year after excavation and "2–4 year-old" if they were examined two to four years after excavation. When we observed cavity usurpa-

tions between cavity users during our survey, we recorded which species were involved. All visits were made during daylight so we have no information on cavity utilization at night. Some GSW cavities were lost due to natural events or logging, and we classified the former as "broken" and the latter as "logged." Line transects for bird censuses were established in both study sites: 50 m wide and 1.4 km long in HKD and 50 m wide and 3.4 km long in HJO. At each study site, line transect surveys were conducted from 05:00 to 08:00 in the morning during late May (1995–1998 for HKD and 1999 for HJO).

RESULTS

1) Cavity loss, reuse by GSWs and availability to SCUs

Through the survey, we found 24 (5, 7, 6, and 6 for 1994, 1995, 1996 and 1997) and 42 (7, 8, 15 and 12 for 1995, 1996, 1997 and 1998) new GSW nests in HKD and HJO, respectively. The proportion of dead trees among the nest trees was significantly higher in HJO (45.2%) than in HKD (4.2%) (Fisher's exact test, $P < 0.01$).

We inspected 59 nest cavities (1 year-old=24; 2–4 year-old=35) in total for HKD (1995–1998) and 42 nest cavities (1 year-old=12; 2–4 year-old=30) for HJO (1999). Some nest cavities or whole trees with nest cavities were lost due to human activity or natural events. The losses amounted to 12.5% of the 1 year-old and 17.1% of the 2–4 year-old cavities in HKD. The primary cause of cavity losses in this area was logging in the course of road or building construction (6 of 8); the other two were lost when trunks broke at a cavity (Fig. 1). In HJO, all cavity losses (16.7% for 1 year-old and 20.0% for 2–4 year-old cavities) were caused by natural events (mainly strong winds) (Fig. 1).

We found four cases of cavity reuse for breeding by GSW (1 in HKD and 3 in HJO, Fig. 1). Cavities were not considered available for SCU when GSWs were using them for nesting.

Finally, we found that the proportions of GSW cavities available for SCU species were 87.5% (1 year-old) and 80.0% (2–4 year-old) in HKD, and 66.7% (1 year-old) and 76.7% (2–4 year old) in HJO.

2) Cavity use by SCUs and nest webs

Cavity-nesting bird species are a major component of the bird communities in both of our study sites. From the line transect surveys, the proportion of cav-

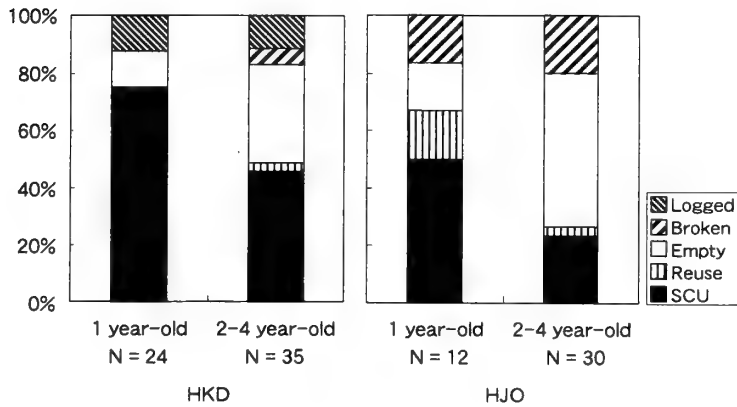


Fig. 1. Status and utilization of 1 year-old and 2-4 year-old GSW cavities in urban (HKD) and suburban (HJO) forests.

ity-nesting bird species among all recorded individuals was 75.5% (total bird density: 8.65/ha) for HKD and 62.0% (5.08/ha) for HJO (Table 1). Two species of PCN, GSW and Japanese Pygmy Woodpecker *Dendrocopos kizuki* were observed at our study sites. For both sites, the GSW was the dominant PCN species (Table 1). Overall, five avian and one mammalian SCU species used 47 (34 for HKD and 13 for HJO) GSW nest cavities (Fig. 2).

Within the available nest cavities, 1 year-old cavities were occupied more frequently than 2-4 year-old cavities (Fisher's exact test, HKD: $P=0.06$; HJO: $P<0.05$, Table 2). The number of nest cavities in the two different "cavity age groups" used by each species at both study sites, elucidating the shift from GSW to SCU, can be seen in Figure 2.

The composition of the "nest webs" differed fundamentally between HKD and HJO. In HKD, avian species that used GSW nest cavities were Tree Sparrow *Passer montanus*, Chestnut-cheeked Starling *Sturnus philippensis* and Nuthatch *Sitta europaea*. The Tree Sparrows and Chestnut-cheeked Starlings were the dominant GSW cavity users and occupied 94.1% (16 for Tree Sparrow and 16 for Chestnut-cheeked Starling) of 34 cavities used by SCUs. Although the density of the Tree Sparrows (4.01/ha) was about five times as high as that of the Chestnut-cheeked Starlings (0.80/ha), we found the occupation rate of the GSWs nest cavities by Chestnut-cheeked Starlings was disproportionately higher than that by Tree Sparrows (G-test, $df=1$, $G=37.4$, $P<0.001$, Fig. 2). One mammalian species (the Flying Squirrel *Pteromys volans*) was the most dominant user of GSW cavities in HJO, followed by avian species (Nuthatch, Great Tit *Parus major* and Russet Spar-

Table 1. Bird density (no/ha) of HKD (averaged 1995-1998) and HJO (1999)

Bird Species		HKD (no/ha)	HJO (no/ha)
PCNBs	<i>Dendrocopos major</i>	0.16	0.20
	<i>D. kizuki</i>	0.01	0.04
	Total PCNBs	0.17	0.24
SCUs	<i>Passer montanus</i>	4.01	—
	<i>Sturnus philippensis</i>	0.80	—
	<i>Parus major</i>	0.65	0.71
	<i>Sturnus cineraceus</i>	0.62	—
	<i>Parus palustris</i>	0.10	0.75
	<i>Ficedula narcissina</i>	0.09	0.24
	<i>Sitta europaea</i>	0.02	0.31
	<i>Parus varius</i>	0.01	0.08
	<i>Passer rutilans</i>	—	0.51
	<i>Parus ater</i>	—	0.08
Total SCUs		6.29	2.68
Others		2.18	2.17
Total		8.65	5.08

row *Passer rutilans*). The Flying Squirrel occupied 61.5% (8 of 13) of the GSW cavities used by SCU.

It is to be noted that 85.7% (1 year-old) and 57.1% (2-4 year-old) of all the available GSW cavities examined were occupied in HKD, while in HJO only 25.0% (1 year-old) and 13.0% (2-4 year-old) were occupied by avian SCU species (Fisher's exact test, 1 year-old: $P<0.005$; 2-4 year-old: $P<0.005$).

The Nuthatch was the only SCU species that used the GSW cavities at both study sites. Although Great Tits were found at both of our study sites, we could not find any nest belonging to this species among the available cavities in HKD. One of the five Great Tit

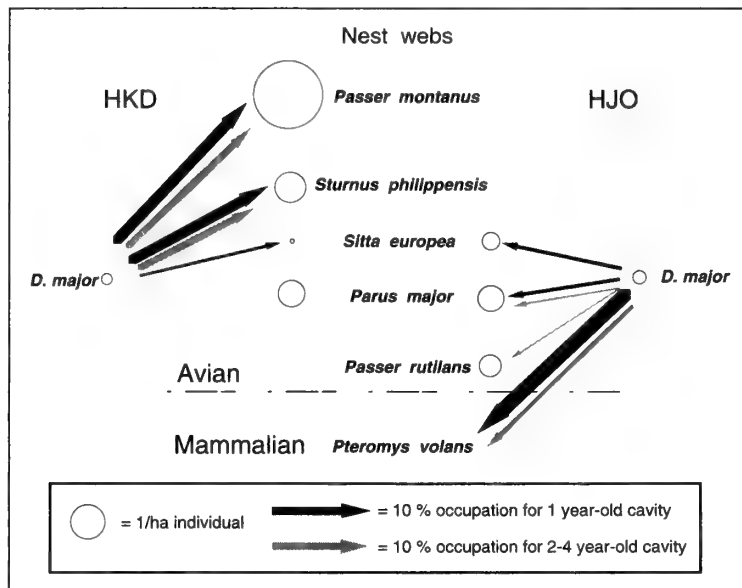


Fig. 2. Turnover of species using GSW nest cavities in urban (HKD) and suburban (HJO) forests. Arrows connect species that use resources provided by GSW. The size of the circles indicates the bird density (no/ha) of each species and the width of the arrows shows the percentage of occupancy of available GSW cavities for each species. The sample sizes for the SCU species are 21 (1 year-old) and 28 (2–4 year-old) for HKD and 8 (1 year-old) and 23 (2–4 year-old) for HJO.

Table 2. Utilization of GSW cavities in relation to nest age in urban (HKD) and suburban (HJO) forests.

Nest age	HKD		HJO	
	1 year	2–4 year	1 year	2–4 year
Occupied	18	16	6	7
Empty	3	12	2	16

nests found in HKD was in a cavity of unknown origin and the others were in natural or artificial holes.

3) Interactions and cavity usurpations

In HKD, cavity usurpations between SCU species were observed. Chestnut-cheeked Starlings drove five pairs of Tree Sparrows out of their nest sites, and Chestnut-cheeked Starlings and Tree Sparrows replaced one and two pairs of Great Tits, respectively.

GSWs aggressively harassed Chestnut-cheeked Starlings, Tree Sparrows, and Great Tits when these species approached their nests. In spite of these attempts to defend their nest sites, 28.6% (6 of 21) of newly excavated GSW nest cavities were usurped by Chestnut-cheeked Starlings. Three of the six pairs whose cavities were taken over attempted to excavate new nest cavities, but the others did not. Only one of the pairs that made new cavities succeeded in raising

their offspring while the others abandoned their nests.

In HJO, we did not observe direct competition between SCU species and GSW for nest cavities.

DISCUSSION

In our study sites, we found that five avian and one mammalian species used GSW cavities. Thus, the GSW may function as a keystone species, in the urban as well as suburban areas of Sapporo, by providing a critical resource—nesting cavities—for SCUs. Woodpecker cavities can enhance breeding success and reduce predation risk (Rendell & Robertson 1989; Li & Martin 1991), and they may provide thermoregulatory advantages for some SCU species, including Flying Squirrels (Carey et al. 1997).

With the exception of the Nuthatch, none of the species using GSW nest cavities in HKD was found to use them in HJO, and vice versa. It is interesting to note that in HKD where the woodland was highly fragmented, the GSW cavities were frequently occupied by avian SCU species, but almost none by mammalian SCU species.

The competition for GSW cavities may be severer in HKD, reflecting its poor habitat quality. In this area Chestnut-cheeked Starling is the largest user of GSW cavities. In HKD, Chestnut-cheeked Starlings

occupied the same number of GSW cavities as Tree Sparrows did, because they are probably the dominant species in competition for the cavities.

In HKD, Chestnut-cheeked Starlings even usurped GSW newly excavated cavities. Ingold (1994) suggested that woodpeckers (Red-bellied Woodpecker *Melanerpes carolinus*, Northern Flicker *Colaptes auratus*, Red-headed Woodpecker *M. erythrocephalus*) can avoid competition with European Starling *Sturnus vulgaris* and may not have suffered reductions in fecundity, because at least some of these pairs were successful in building new nests later in the season. However, the success rate of the re-nesters was only 17% (1 of 6) in HKD; pairs of GSW were unable to avoid competition with Chestnut-cheeked Starlings and suffered apparent reductions in fecundity.

In HJO, the Flying Squirrel was the main user of GSW cavities. In North America, Flying Squirrels are seen as major predators or competitors of nesting Red-cockaded Woodpeckers *Picoides borealis* (Loeb 1993; Loeb & Hooper 1997; but see Mitchell 1999). Dominant competitors (e.g. Chestnut-cheeked Starlings or Flying Squirrels) may affect utilization and nest-site selection of other SCU species as well as PCNs through their ability to win the competition for cavities. Johnsson et al. (1993) found that the most competitive species, Jackdaws *Corvus monedula* usually used the best old Black Woodpecker *Dryocopus martius* holes, while other subordinate species used inferior holes in a Swedish forest. Further research on species-specific cavity selection and ability of competing for nest cavities would help to determine functional relationships between GSW and SCU species.

The significant difference in the utilization frequencies between 1 year-old and 2–4 year-old cavities suggests that the suitability of GSW nest cavities deteriorates with time elapsed after excavation. Some of the old GSW nest cavities could obviously not be used by SCU species any more because they were clogged with mushrooms, or because the size and shape of the entrance had changed as the living tissues of the tree around it kept growing. Old GSW cavities in living trees seemed to have narrower openings than newly excavated ones, probably due to the lateral growth of the stems.

Another factor that has been reported to prevent repeated use of nest holes is infection with pathogenic organisms or parasites. If old nest material contains larger parasite loads (Perrins 1979; Møller 1989), the lower occupation rate for older (2–4 year-old) cavities might be an indirect effect of parasite avoidance.

In addition to losses of GSW cavities due to natural events, human activities can be of major importance, especially in or near urban areas. Human impact is responsible mostly for decreases in the number of available nest cavities, whereas natural processes influence also the suitability of a given nest hole for repeated use.

Most woodpecker species use trees for nesting, foraging and communication, and they are extremely sensitive to extensive forest harvesting (Winkler et al. 1995). If local extinction of a keystone species, such as GSW, occurred, we predict that the wildlife community will face a catastrophic ecological cascade. To maintain the diversity of wildlife in urban areas, city planners should protect existing GSW cavity trees and maintain a sustainable breeding habitat for continued production of new cavities.

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ORIGINAL ARTICLE

Foraging niches of introduced Red-billed Leiothrix and native species in Japan

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Abstract In Kyushu, southwestern Japan, the introduced population of the Red-billed Leiothrix *Leiothrix lutea* has increased rapidly and its range expanded considerably since early 1980s. In order to clarify the influences of Red-billed Leiothrix on native bird species, we examined the similarities and differences in foraging patterns among species occurring in a deciduous broadleaved forest on the Ebino Plateau, during the breeding seasons from 1997 to 2000.

Leiothrix foraged in a lower vegetational layer with bamboo, intermediate in height between the foraging levels of the Japanese Bush Warbler *Cettia diphone* and various *Parus* species. Foraging height, extent of foraging on deciduous trees and foraging technique were major factors best distinguishing Leiothrix from native species. Segregation of foraging niche was distinct and no apparent niche shift, due to invasion of the new species, was detected. Aerial insects tended to be more abundant just above bamboo, mainly about one meter above the canopy, than above bare ground. Thus, jumping, a specific technique used by Leiothrix, is effective for capturing aerial insects or agile invertebrates resting on leaves and twigs. Aerial insects were found to be abundant in the foraging space preferred by Leiothrix. Gleaning and hanging, techniques mainly used by native species, are suitable for capturing prey of low mobility such as Lepidoptera larvae. Probably due to morphological constraints, *Parus* spp. and Japanese Bush Warblers seldom foraged by jumping, indicating that they exploit quite different food resources from those utilized by Leiothrix despite their foraging spaces overlapping to some extent.

In the deciduous broadleaved forests of Kyushu, an avian guild of foraging aerial insects in intermediate and lower layers of the forests is poor. Such a community may be subject to the successful invasion of the Red-billed Leiothrix into native forests.

Key words Ecological isolation, Foraging niche, Interspecific competition, Introduced birds, *Leiothrix lutea*

The Red-billed Leiothrix *Leiothrix lutea*, originally occurring from southern China to the western Himalayas (Ali & Ripley 1972; Long 1981; Lever 1987; MacKinnon & Phillipps 2000), has been introduced to Japan where many naturalized populations have been found in deciduous broadleaved forests in central and southwestern Japan since the early 1980s (Tojo 1994; Eguchi & Amano 2000). The expansion of its range and the increase in its numbers has been particularly remarkable in Kyushu, southwestern Japan (Eguchi & Amano 2000). Where it is indigenous, the Red-billed Leiothrix occurs in various habi-

tats including deciduous broadleaved forests, bamboo thickets, tea plantations, and secondary forests near human habitations from 900 m to 3,000 m asl (De Schauensee 1984; Long 1987). In Japan, Leiothrix inhabits deciduous broadleaved forests with a dense understory of dwarf bamboo, and utilizes low layers of forest vegetation (Eguchi & Masuda 1994). In Kyushu, the habitat of Leiothrix overlaps that of a number of native species including the Japanese Bush Warbler *Cettia diphone*, Long-tailed Tit *Aegithalos caudatus* and various *Parus* species such as the Great Tit *Parus major*, Coal Tit *P. ater*, Varied Tit *P. varius*, and Willow Tit *P. montanus* (Eguchi & Masuda 1994). These native species also occur widely in deciduous broadleaved forests in Japan (Nakamura

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1970, 1978).

Introduced birds may diminish the number of native species through interspecific competition (Moun-tainspring & Scott 1985; Jones 1996). Usually introduced bird species succeed in establishing self-maintaining populations only in habitats disturbed by people (Case 1996) where they compete only with introduced species (Moulton & Pimm 1983; Moulton 1993). The Red-billed Leiothrix has, however, invaded native forests in Japan and has increased rapidly in number. As a result of this, interspecific competition between Leiothrix and native species is likely in Japan.

Instances of interspecific competition are difficult to detect (Lodge 1993). One approach to clarifying such competition is the study of habitat selection (Sol et al. 1997). If competition exists, two major resources, nest-sites and food, may be limiting. Amano and Eguchi (2002) revealed differences in nest-site characteristics between the Red-billed Leiothrix and Japanese Bush Warbler in forest, and suggested that competition between them for nest-sites did not exist, however, no quantitative evaluation has so far been made of either their food resources or their foraging spaces.

Foraging niches are highly segregated among sympatric Paridae (Gibb 1954; Hogstad 1978; Morse 1978; Nakamura 1970, 1978; Ogasawara 1970, 1975). Such segregation is partly derived from interspecific competition (Lack 1971). The Willow Tit, for example, often shifts its foraging height when it occurs in mixed-species flocks in the presence of dominant Great Tit (Alatalo 1981). Niche shift, in the presence of competitive species, has also been observed in another Paridae community with a different species composition (Herrera 1978). Thus a shift of foraging location is important evidence of interspecific interference competition.

In this paper, we aim to clarify the patterns of foraging space and foraging techniques of the introduced Red-billed Leiothrix and of several sympatric native forest bird species. In addition, we will show Leiothrix utilizes a unique foraging space that native species rarely use.

STUDY AREA AND METHODS

1) Study area

The study was conducted from April to September during each breeding season from 1997 to 2000, on the Ebino Plateau, southwestern Kyushu, Japan

(1,200 m in elevation; 31°56'N, 130°51'E). The study area was situated in a mixed forest (16 ha) composed of *Abies firma*, *Tsuga sieboldii*, *Pinus densiflora*, *Quercus crispula*, *Hydrangea paniculata*, *Symplocos coreana*, and *S. myrtacea*. The shrub layer was dominated throughout the forest by the dwarf bamboo *Sasamorphia borealis* (ca. 2 m in height). Only small patches of ground were bare. A road, approximately 10 m wide ran through the forest. The annual mean precipitation exceeds 5,000 mm on the Ebino Plateau, of which more than one-third occurs during June and July (data from Miyazaki Branch, Weather Service of Japan).

The Red-billed Leiothrix was first recorded in this area about twenty years earlier (N. Kamitanigawa pers. comm.). This species breeds from April to September and emigrates to lower areas for the winter (pers. obs.). During the breeding season, six resident native species regularly occur in the same habitat as Leiothrix; four Paridae (Great, Varied, Willow, and Coal tits), Long-tailed Tit, and Japanese Bush Warbler (see Appendix 1 for the morphological characteristics of these species). Other sympatric species, including two trunk-specializing foragers (Japanese Pygmy Woodpecker *Dendrocopos kizuki* and Nuthatch *Sitta europaea*), and one sallying forager (Blue-and-white Flycatcher *Cyanoptila cyanomelana*), were excluded from the analysis, because of their low abundance, scarcity of observations, or great difference in foraging techniques from Leiothrix.

2) Observation of foraging birds

We searched for birds as we walked along forest paths. When we encountered birds foraging, we recorded the following information: species, time of day, foraging height, height of trees on which birds foraged, foraging location, foraging technique and whether or not there was a dwarf bamboo understory beneath/around the foraging location. We compared the percentage occurrence of foraging above or inside dwarf bamboo, because small patches of dwarf bamboo and of bare ground are abundant in the study area. We divided foraging location into six categories: foliage (including leaf, flower, fruit, bud and twig), branch, trunk, undergrowth (defined as shrubs if they were 2 m tall or shorter), ground, and air. Foraging techniques were defined as follows: (1) glean, a technique in which a prey item was picked up from a substrate by a standing or walking bird; (2) jump, a technique in which a bird jumped upon a prey item and snatched it from a substrate; (3) hang, a tech-

nique in which a bird hanging on a substrate picked a prey item; (4) hover, a technique in which a hovering bird picked a prey item from a substrate; (5) hawk, capturing an aerial prey item in the air; (6) peck, a technique in which a bird pecked a substrate and picked a subsurface prey item; and (7) others, other miscellaneous techniques were included. Heights were estimated to the nearest meter.

We followed individual birds as long as they remained in sight, because the foliage was dense and visibility in the forest was poor. We changed individuals after one foraging record had been collected. If only single birds or pairs were present, we collected two further foraging records from each bird once they had changed foraging trees or foraging locations. No more than one record was collected for an individual while in the same tree.

Observations were made from 0830 to 1700. For the analyses, data were pooled for all individuals of each species, for all months and years.

3) Measurement of abundance of invertebrate prey

We compared the abundance of aerial insects between areas above dwarf bamboo and areas away from dwarf bamboo. In May 1997, we set 500-ml aluminum cans daubed with sticky glue 3–4 m above the ground as traps. Pairs of traps were set, one of each pair was set above dwarf bamboo and the other was set 10 m away, and away from dwarf bamboo (Fig. 1a). In total, 50 pairs of traps were distributed throughout the study area. Two days after setting

them, we recovered the traps and collected, and counted, all the invertebrates stuck to their surfaces. In 2000, in order to assess the vertical distribution of aerial insects above dwarf bamboo, we set sticky traps (commercial sticky fly traps; 70×3.5 cm) 3 m and 6 m above the ground, and 1 m and 4 m above the canopy of dwarf bamboo (Fig. 1b). These traps were set at 15 points for two days. Then, after recovering them, we counted the numbers of invertebrates on each trap. These invertebrates were identified either to the family or order level and divided into two size classes; larger than 5 mm but smaller than 10 mm, and 10 mm or larger.

RESULTS

1) Foraging height and tree height

There were significant interspecific differences in foraging heights at which birds foraged ($F_{6,829} = 12.67$, $P < 0.0001$, ANOVA, Fig. 2). The Red-billed Leiothrix foraged mainly 4 ± 2 m (median and 25–75% percentiles) above the ground, and the Japanese Bush Warbler foraged mainly 3 ± 2 m above the ground, although the difference between these two species was not significant ($P = 0.23$, Scheffé's test). The Varied Tit and Coal Tit frequently foraged in the upper layer of the forest above 8 m, significantly higher than Leiothrix ($P < 0.001$ for each comparison, Scheffé's test). There were no significant differences in foraging height, however, between Leiothrix and Long-tailed Tit ($P = 0.97$, Scheffé's test),

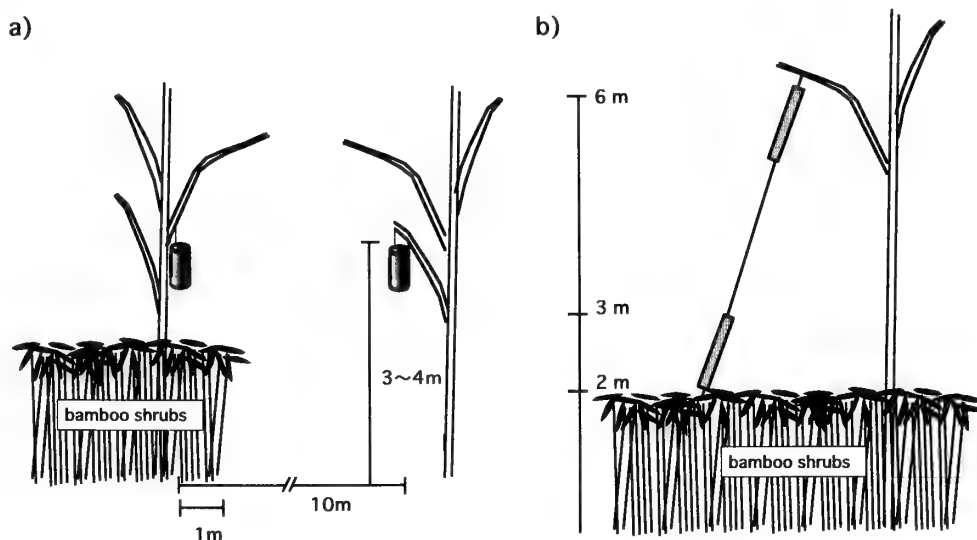


Fig. 1. Traps for collecting aerial insects. a) 500 ml can traps daubed with sticky glue, b) sticky ribbon traps (70 × 3.5 cm) set at 1 m and 4 m above a canopy of bamboo shrubs.

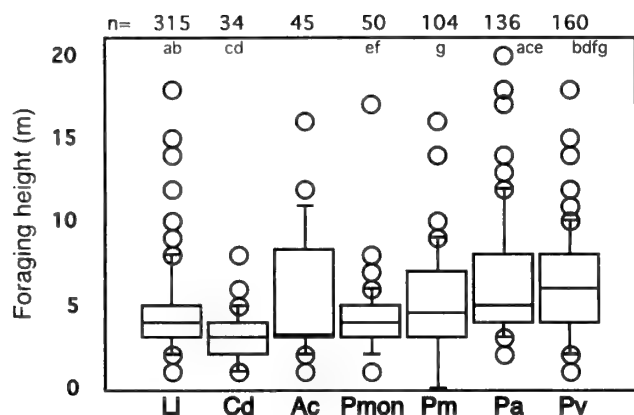


Fig. 2. Foraging heights of each species. L, *Leiothrix lutea*; Cd, *Cettia diphone*; Ac, *Aegithalos caudatus*; Pmon, *Parus montanus*; Pm, *P. major*; Pa, *P. ater*; Pv, *P. varius*. Crossbars represent 50% (median), boxes 25–75% percentiles and bars 10–90% percentiles. Circles are outliers. Pairs of a same character indicate a significant difference; a $P < 0.001$, b, c, d $P < 0.0001$, e, f $P < 0.01$, g $P < 0.05$, using Scheffé's F test.

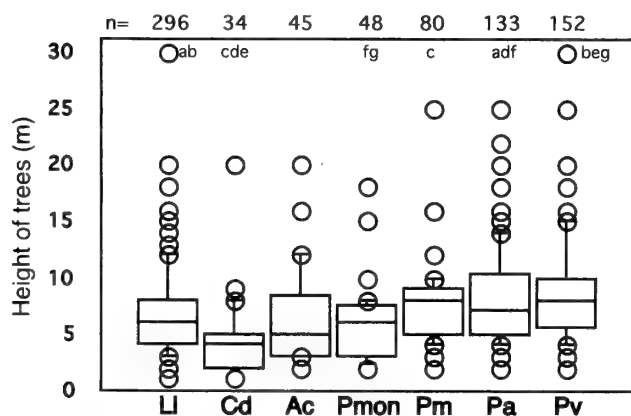


Fig. 3. Heights of trees in which each species foraged. See Fig. 2 for abbreviations. Pairs of a same character indicate a significant difference; a, g $P < 0.01$, b, e $P < 0.0001$, c, f $P < 0.05$, d $P < 0.001$, using Scheffé's F test.

Willow Tit ($P = 0.98$) or Great Tit ($P = 0.98$).

There were significant differences among bird species in the height of trees in which they foraged ($F_{6, 788} = 10.90$, $P < 0.0001$, ANOVA, Fig. 3). Japanese Bush Warblers mainly used trees or shrubs lower than 5 m. Varied and Coal tits used trees that were significantly higher than those used by *Leiothrix* ($P < 0.0001$ and $P < 0.01$, respectively, Scheffé's test). There were no significant differences, however, between the heights of trees selected by *Leiothrix* and the remaining species ($P = 0.20$ Japanese Bush Warbler; $P = 1.00$ Long-tailed Tit; $P = 0.89$ Willow Tit;

and $P = 0.98$ Great Tit; all Scheffé's test).

2) Foraging location

The Red-billed *Leiothrix*, as well as the other species, mainly foraged in deciduous broadleaved trees, while Long-tailed Tits and Coal Tits also frequently foraged in coniferous trees (Fig. 4a). Japanese Bush Warblers often foraged in the undergrowth, mainly in dwarf bamboo.

Variation in foraging location was rather small (Fig. 4b). Each species foraged in foliage, mainly from leaves and twigs. In substrates other than foliage, Japanese Bush Warblers, Willow, and Great tits often foraged in the undergrowth or on the ground, while Coal and Varied tits foraged on branches and trunks. Great Tits also frequently caught prey in the air (aerial catching).

Both Red-billed *Leiothrix* and Japanese Bush Warbler exclusively used that part of the forest where there was dwarf bamboo in the understory, while the levels of occurrence in such areas was relatively low for the Long-tailed and Great tits, and intermediate for Willow, Coal, and Varied tits (Table 1). The overall difference was significant among species ($df = 6$, $\chi^2 = 150.5$, $P < 0.0001$).

3) Foraging technique

Species varied considerably in their foraging techniques (Fig. 4c). The major technique used by each species was gleaning. Red-billed *Leiothrix*, however, often foraged by jumping on prey items. Hanging was used frequently by Long-tailed, Willow, Coal, and Varied tits. Willow Tits and Coal Tits often pecked at buds and flowers, and also picked prey items. Great Tits also caught aerial insects gathering around flowers before leaving out in spring, whereas Japanese Bush Warblers foraged exclusively by gleaning.

4) Vertical distribution of invertebrates

From the results referred to above, it is clear that the Red-billed *Leiothrix* mainly used the lower layer of the forest with dwarf bamboo in the understory and it foraged more frequently by jumping than any of the other species. Foraging by jumping may be an effective technique for catching aerial insects resting on leaves or twigs. *Leiothrix* often foraged just above dwarf bamboo. Although there was no significant difference in the abundance of small invertebrates (5–10 mm), large Mecoptera, a dominant taxon among large (≤ 10 mm) invertebrates (and eaten by *Leiothrix*,

Foraging niche of the Red-billed Leiothrix

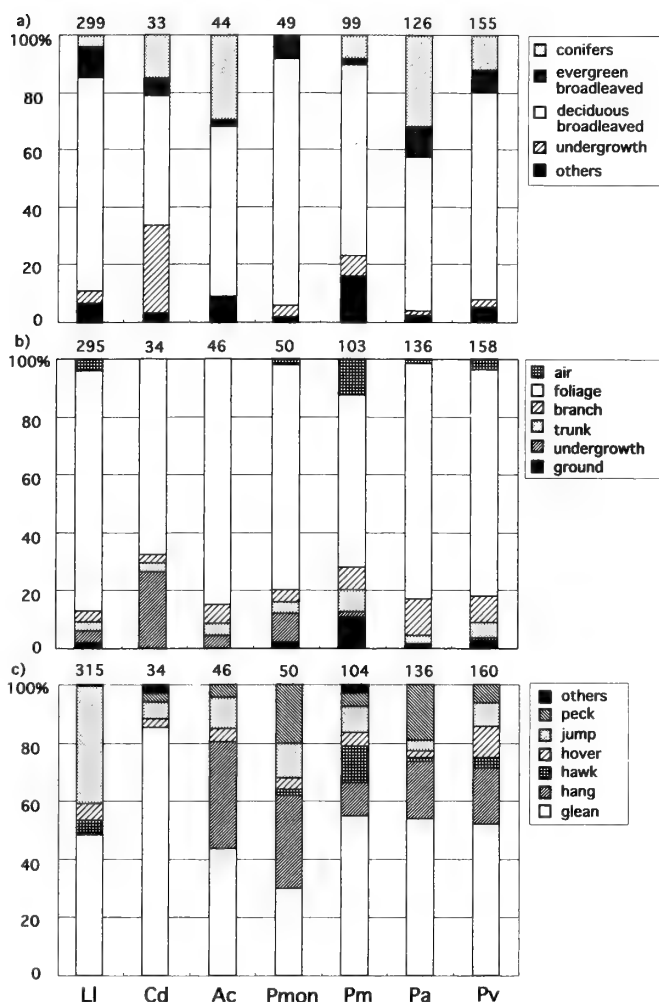


Fig. 4. a) Use of trees by each species, b) use of substrates by each species, c) foraging techniques used by each species. Figures above columns are the numbers of observations. See Fig. 2 for abbreviations.

Table 1. Percent occurrence of foraging above or inside of bamboo shrubs.

	<i>Leiothrix lutea</i>	<i>Cettia diphone</i>	<i>Aegithalos caudatus</i>	<i>Parus montanus</i>	<i>Parus major</i>	<i>Parus ater</i>	<i>Parus varius</i>
Yes	89.2	88.2	36.6	66	40.8	60.3	63.3
No	10.8	11.8	63.4	34	59.2	39.7	36.7
No. of observations	295	34	41	50	103	136	158

pers. obs.), were more abundant just above dwarf bamboo shrubs than above bare ground (0.44 ± 1.07 vs. 0.12 ± 0.39 ; mean number \pm SD; $N=50$, $P=0.048$, Wilcoxon signed rank test).

In a comparison between the abundance of invertebrates in an upper layer (4 m above dwarf bamboo canopy) and a lower layer (1 m above dwarf bam-

boo), the total abundances of both small and large invertebrates were greater in the lower level than in the upper in each month, but not significant (see Fig. 5). The only exception was for the abundance of small invertebrates in May (Fig. 5a). At taxonomic levels, the abundances of invertebrate in the lower layer also tended to be greater than in the upper layer, but the

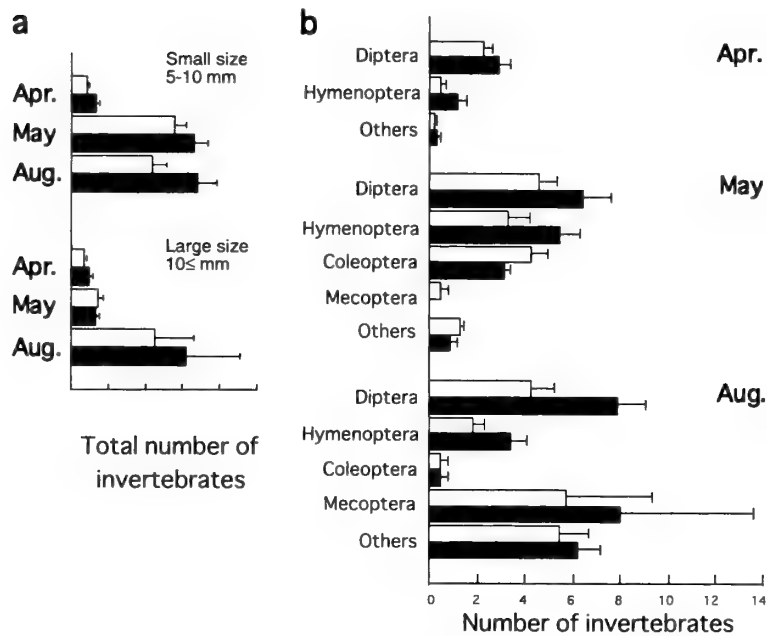


Fig. 5. Abundances of invertebrates (mean \pm SE) collected with sticky ribbon traps. a) the total numbers; b) the number of each taxon. Open bars and solid bars indicate upper traps and lower traps, respectively. See text for results of statistical tests.

differences were not significant (Wilcoxon signed rank test with sequential Bonferroni modification for multiple tests; Fig. 5b).

DISCUSSION

1) Differences in foraging patterns

In this study, foraging height was highest in the Coal Tit and Varied Tit, lowest in the Japanese Bush Warbler, and intermediate in the Red-billed Leiothrix. Among the other small woodland birds, Varied Tits and Coal Tits foraged in the highest layer, Willow Tits and Great Tits in the intermediate and lower layers and Long-tailed Tits foraged at a wide range of heights. Despite limited sample sizes, a similar pattern in foraging has been observed in other regions of Kyushu where *Leiothrix* has invaded (e.g. Mt. Hikosan and Mt. Ichibusayama, Eguchi & Masuda 1994; Kikuchi Glen, pers. obs.).

Data on the utilization pattern of foraging space among small woodland birds during the breeding season are limited outside Kyushu (but see Nakamura 1970; Ogasawara 1975). There is, however, a similar pattern of foraging space use among Paridae and other small woodland species during the breeding season in various areas in Japan; e.g., Kyushu (this study), central Japan (Nakamura 1970) and northern

Japan (Ogasawara 1975). For example, Varied Tit and Coal Tit forage in the upper layer of the forest, while Great Tit and Willow Tit forage in the middle and/or lower layers. Long-tailed Tit has a broad foraging range, but is found especially in the lower layers of deciduous broad-leaved trees and in the middle and higher layers of coniferous trees in a mixed forest with sparse undergrowth, in central Japan (Nakamura 1970). Given the similarities in the use of foraging space between this study (where *Leiothrix* occur) and those elsewhere, it appears that there is no distinct shift in use of foraging space in any species in the presence of *Leiothrix*. Hence, it is unlikely that the segregation in use of foraging space observed among species in Kyushu has been brought by interspecific competition with introduced *Leiothrix*.

Ecological segregation can be achieved by employing unique foraging techniques, such as jumping to capture prey, which is commonly used by the Red-billed *Leiothrix*, but rarely used by other species. *Leiothrix* flies quickly from branch to branch, whereas tits and bush warblers hop or walk relatively slowly in the foliage (pers. obs.). Such movement is related to the main foraging techniques adopted by each species. It is likely that the foraging space utilization and the foraging technique of the Red-billed *Leiothrix* are both well adapted to foraging for aerial

insects or agile invertebrates on leaves and twigs. Indeed, this species often provided aerial insects such as Mecoptera to its nestlings (pers. obs.).

In contrast to Leiothrix, Paridae species foraged exclusively by gleaning and hanging, which suggests that these species adopt a foraging technique suitable to capturing prey of low mobility such as Lepidoptera larvae on leaves and twigs. In southern Japan, Great Tit and Varied Tit mainly feed Lepidoptera larvae and spiders to their nestlings (Eguchi 1980, 1985). These relatively inactive prey items can be captured easily by gleaning. Tits and bush warblers are less able to capture aerial prey even when it rests on a leaf or twig. Gleaning is also the common foraging technique reported for Paridae and Long-tailed Tits in other areas, whereas jumping to capture prey is rarely reported (Nakamura 1970, 1978; Ogasawara 1970, 1975).

2) Morphological constraints

Morphological characters are closely related to ecological characters in some restricted taxa (Leisler & Winkler 1985; Wiens 1989). Morphological constraints may restrict the range of foraging techniques adopted by any given species. A long bill, for example, is suitable for capturing and firmly grasping aerial insects or those of high mobility, while short bills are found predominantly among gleaners (Leisler & Winkler 1985). The Red-billed Leiothrix has a long bill in comparison with other sympatric species, except for the Japanese Bush Warbler. While on the one hand the Red-billed Leiothrix has a relatively wide tail and the extremities of the outermost rectrices curve outwards, which may enhance its manoeuvrability in the air, on the other hand, its large dumpy body may be less suited to moving among leaves for gleaning. Shorter wings relative to body weight of Leiothrix (see Appendix) are not suited to hawking aerial insects in the air, either. The Japanese Bush Warbler has a long bill and long tarsi, as does Leiothrix, but the bush warbler has a rather slender body, which is perhaps related to its habit of clinging to stems of dwarf bamboo. Indeed, the bush warbler foraged exclusively in dwarf bamboo during this study. Thus, due to morphological constraints, the foraging space and foraging technique of the Red-billed Leiothrix were quite different from both the Japanese Bush Warbler and Paridae species. Because the difference in foraging pattern was great, it is unlikely that there is severe interspecific competition for food resources between the Red-billed Leiothrix and na-

tive species.

3) Invasion by the Red-billed Leiothrix

Eguchi and Masuda (1994) showed that the Red-billed Leiothrix mainly inhabits deciduous broadleaved forests with dense dwarf bamboo in the understory in Kyushu, and that its foraging microhabitat is segregated from those of sympatric species. They speculated that the poor species diversity in the avifauna in the lower, shrub layer of the forest is one of the factors contributing to this species' successful invasion and range expansion in Kyushu. In this study too, the Red-billed Leiothrix was found to mainly forage in the lower layer of the deciduous broadleaved forest with dwarf bamboo in the understory.

Sampling of invertebrates with sticky traps revealed that the abundance of aerial insects tended to be higher in the lower layer of the forest just above the dwarf bamboo canopy, than in the upper layer. In such a foraging space, Leiothrix captured aerial insects by jumping. Although other species, such as Long-tailed Tits and Willow Tits, often foraged in the same foraging space, they seldom used jumping as a foraging technique. The Japanese Bush Warbler mainly foraged at lower heights than Leiothrix and seems to forage primarily in dwarf bamboo, being found there in most of our observations. Even when they occur in the same foraging space, Leiothrix and Paridae species may prefer different prey. The food resource just above dwarf bamboo, consisting mainly of aerial insects, may be a reserved resource for the Red-billed Leiothrix.

In central Japan, there are many species specializing to foraging aerial insects such as *Muscicapa* flycatchers, Narcissus Flycatcher *Ficedula narcissina*, Blue-and-white Flycatcher, Paradise Flycatcher *Therapsiphne atrocaudata*, etc. (Agency of Environments 1981; Ornithological Society of Japan 2000). These species mainly capture aerial insects in the intermediate vegetation layer of the forest or among the tree canopy. Only one of these species, however, the Blue-and-white Flycatcher, preys on aerial insects in the forests where the Red-billed Leiothrix has invaded in Kyushu (Eguchi & Masuda 1994, pers. obs.). We postulate that the Red-billed Leiothrix has successfully invaded and increased in deciduous broadleaved forests in Kyushu, by virtue of the relatively low diversity of sallying and hawking bird species foraging for aerial insects in such habitats.

In this study, we found no evidence of any severe direct interspecific competition between introduced

Red-billed Leiothrix and native species. Amano and Eguchi (2002) have suggested, however, that indirect interference may occur, through increase numbers of Red-billed Leiothrix drawing predators to dwarf bamboo, a habitat in which the Japanese Bush Warbler nests, and that increased visits by predators may result in lowered breeding success of the Japanese Bush Warbler. Further studies on the interactions between invasive and native species, including field experiments such as the removal of dominant species (Martin & Martin 2001), are needed.

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Appendix. Measurements of body size for each species studied. Means with SD are shown. Males and females of Japanese Bush Warblers are shown separately because of a great sexual dimorphism in size.

Species	N	Wing length	Tail length	Tarsus length	Bill length	Body weight	WL/log (BW)	TL/log (BW)	TRL/log (BW)	BL/log (BW)	WL/TRL
<i>L. lutea</i>	222	67.3±2.5	58.5±2.4	24.8±1.1	15.8±0.9	21.9±1.3	21.8±0.8	19.0±0.8	8.0±0.4	5.1±0.3	2.7±0.1
<i>C. diphone</i> male	14	65.6±2.0	67.0±3.6	25.0±1.2	5.6±2.1	18.5±1.5	22.5±1.1	23.0±1.5	8.6±0.4	5.4±0.7	2.6±0.2
<i>C. diphone</i> female	18	53.8±3.3	53.7±6.0	22.5±1.7	5.5±2.4	11.5±1.5	22.1±1.4	22.1±2.3	9.3±0.7	6.4±1.0	2.4±0.2
<i>A. caudatus</i>	5	55.2±1.3	65.8±12.6	17.1±1.1	8.6±1.3	8.1±1.3	26.6±1.4	31.9±7.4	8.3±1.0	4.1±0.3	3.2±0.3
<i>P. montanus</i>	3	57.7±7.1	54.3±3.2	17.3±1.5	10.8±0.4	10.9±0.8	24.2±2.7	22.8±1.7	7.2±0.7	4.5±0.1	3.3±0.2
<i>P. major</i>	12	65.1±2.5	58.5±5.9	19.3±2.0	11.4±0.9	14.1±1.1	24.6±1.0	22.1±2.1	7.3±0.9	4.3±0.3	3.4±0.3
<i>P. ater</i>	6	59.4±4.6	46.1±5.1	16.9±1.5	9.8±1.2	9.2±1.2	26.9±2.2	20.8±1.4	7.7±0.6	4.4±0.6	3.5±0.4
<i>P. varius</i>	8	75.5±4.4	54.3±4.1	19.3±1.0	13.0±0.9	16.6±0.8	26.9±1.5	19.3±1.4	6.9±0.4	4.6±0.3	3.9±0.3

ORIGINAL ARTICLE

Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources

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Abstract I examined the effects of arthropod abundance and of bird foraging techniques on the tree species preferences of seven insectivorous bird species in a temperate deciduous forest. It is hypothesized that bird species with a wide range of foraging techniques respond more flexibly to the spatial distribution and seasonal change of prey than those with specialized foraging techniques. This hypothesis was supported by the fact that tits, bird species with a wide range of foraging techniques, changed their techniques when foraging in tree species with different foliage structures. They also used various tree species in late summer when food requirements increased owing to the addition of nestlings and fledglings. Bird species with a narrow range of foraging techniques, such as flycatchers and white-eyes, did not change their techniques among tree species and had strong tree species preferences in all research periods.

Key words Foliage structure, Prey abundance, Tree species preference, Variety of foraging technique

Tree species diversity is one of the most important habitat factors determining bird species diversity in temperate forests, because diverse composition of tree species should facilitate the coexistence of different species of birds (Holmes et al. 1979; Rice et al. 1984; Hino 1985). However, the mechanism of coexistence has not been sufficiently understood. Although many studies have shown different use of tree species among insectivorous birds (e.g., Hartley 1953; Nakamura 1970; Morse 1978; Recher et al. 1991), most such studies have not surveyed the availability of food for birds on different tree species (but see Holmes & Robinson 1981; Diaz et al. 1998; Hino et al. 2002). The abundance and distribution of prey, and the foliage structure, which vary among tree species, influence prey detectability and accessibility by birds (Holmes & Schultz 1988). Thus, the prey availability for each bird species must be determined separately for each tree species. Since different tree species provide different foraging opportunities for

birds, tree species composition within a forest should influence bird species composition and diversity (Holmes & Schultz 1988).

Prey abundance for birds varies among tree species and changes temporally during the breeding season (Feeny 1970; Nager & van Noordwijk 1995; Dias & Blondel 1996; Murakami 1998). Foraging techniques, determined by morphological characteristics of each bird species (Moreno & Carrascal 1993; Carrascal et al. 1995), affect bird preferences for foraging habitat (Nakamura 1978; Holmes and Schultz 1988; Hino et al. 2002). Different foliage structure among tree species often requires foraging birds to use different foraging techniques (Whelan 1989). Under these circumstances, we hypothesize that birds with a variety of foraging techniques can respond flexibly to temporal change and spatial distribution of food abundance. So far, few studies have examined this hypothesis (but see Hino et al. 2002; Murakami 2002).

This study examined the use of tree species and the foraging techniques of seven forest bird species in temperate deciduous forest. Temperate deciduous forests are most appropriate for the study of tree species preferences of birds because the number of

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tree species is not as high as in tropical forest and not as low as in coniferous boreal forest. I analyzed how seasonal changes in tree species preferences of birds were affected by their foraging techniques, by prey abundances and by the foliage structure of trees.

MATERIALS AND METHODS

1) Study site

This research was conducted in the experimental forest of the Hokkaido Research Center, the Forestry and Forest Products Research Institute, located in Sapporo, Japan (42°59'N, 141°23'E). A 9 ha-study area was established in a secondary deciduous broadleaved forest, which had been burned about 70 years ago. The vegetation was surveyed in fifteen 25m-square plots selected randomly in the study area. Species, number of individuals, and diameter at breast height (DBH) were recorded for all trees. Tree species composition was calculated as the percentage of basal area given by DBH. The dominant tree species are Japanese White Birch (*Betula platyphylla*, 46.2%), Oak (*Quercus mongolica* v. *grosseserratus*, 13.7%), Casterarealia (*Kalopanax pictus*, 10.0%), Printed Maple (*Acer mono*, 5.0%), Japanese Linden (*Tilia japonica*, 5.0%) and Alder (*Alnus hirsuta*, 4.3%). The understory is dominated by a high density of dwarf bamboo (*Sasa senanensis* and *S. kurilensis*) 0.5–2 m in height.

Budding of most trees starts in early May. Research was conducted from 21 May to 5 July in 1992 and from 22 May to 19 June in 1993. Five research periods of two weeks each were established for bird observations and prey sampling: 92-1 (21 May–5 June), 92-2 (6 June–20 June), 92-3 (21 June–5 July) in 1992; 93-1 (22 May–5 June), 93-2, (6 June–19 June) in 1993.

2) Bird foraging

The target species were seven insectivorous bird species. These were three resident species: Great Tit (*Parus major*), Marsh Tit (*P. palustris*) and Long-tailed Tit (*Aegithalos caudatus*), and four migrant species appearing in May: Japanese White-eye (*Zosterops japonica*), Narcissus Flycatcher (*Ficedula narcissina*), Eastern Crowned Leaf Warbler (*Phylloscopus coronatus*) and Brown Flycatcher (*Muscicapa dauurica*). Observations of Marsh Tits may have included Willow Tits (*Parus montanus*), which were very low in abundance, because those two species are difficult to distinguish in the field. The data on fledg-

lings were excluded from the analysis.

I observed bird foraging behavior through binoculars (8–16 times zoom) from 0500 to 1000 except on rainy days or on days with strong wind. When a foraging bird was encountered, I followed it as long as possible, and recorded the tree species it visited and its foraging techniques. Foraging techniques were classified into three types: perch-gleaning (gleaning prey from leaves or branches while perching on branches); hang-gleaning (taking prey from leaves or twigs by hanging upside down from twigs or leaves); and hovering. In this study, one tree individual was regarded as one patch for foraging. Even if birds searched but did not capture prey on a tree during the observation, thus, the datum was dealt with as one sample of use of the tree species. Even if a bird foraged many times successively on the same tree, the datum was dealt with as one sample. When a bird foraging on a particular tree species flew to the same tree species less than 3 m away, or with and overlapping crown, or when a bird being followed was lost to sight for a few seconds in foliage (when no other conspecific birds were found nearby), the datum was also dealt with as one sample. In contrast, all data relating to foraging techniques were dealt with as independent samples even when foraging occurred successively on the same tree. No more than 10 samples of foraging technique observations were taken from each individual bird. The data included both feeding nestlings or fledglings and foraging for themselves. To avoid bias from repeated observations of the same individuals, I collected the data while walking steadily within the study area.

The preferences of birds for each tree species were calculated using Ivlev's electivity index (Ivlev 1955): $E = (p_i - r_i) / (p_i + r_i)$, where p_i represents the proportions of the i th tree species used by a particular bird species and where r_i is the proportion of tree species composition occupied by the i th tree species in the study area. Following Holmes and Robinson (1981), the 'tree preference index' was obtained as a sum of the percentage deviations of bird use from the tree species composition for six dominant species (*B. platyphylla*, *Q. mongolica*, *K. pictus*, *A. mono*, *T. japonica*, *A. hirsuta*). This index shows that the higher the value is, the more specialized the bird is in tree species use. The similarity in tree species use between two bird species was calculated with Pianka's index (Pianka 1973):

$$\alpha_{jk} = \sum_i p_{ij} \cdot p_{ik} / \left(\sqrt{\sum_i (p_{ij})^2} \sqrt{\sum_i (p_{ik})^2} \right),$$

where p_{ij} and p_{ik} are the proportions of the i th tree species used by the j th and the k th bird species, respectively. The similarity between tree species use by birds and tree species composition in the study plot was also calculated using Pianka's index. The cluster analyses were performed using Mountford's method (Mountford 1962). The variation in foraging techniques was shown using Shannon's H' (Shannon & Weaver 1949): $H' = -\sum q_j \log_2 q_j$, where q_j is the proportion of the j th foraging technique.

3) Arthropod sampling

Spiders and insects were searched for, counted and measured, at 1–2 m in height in four species of trees (*A. mono*, *A. hirsuta*, *Q. mongolica* and *T. japonica*) in 1992 and six species (addition of *B. platyphylla*, and *K. pictus*) in 1993. Each sample consisted of 400 leaves with branches and twigs for five of these tree species, with the exception of *K. pictus* of which 50 leaves were sampled owing to their very large size. Seven units were sampled for each tree species in all research periods in 1992, ten in 93-1, and nine in 93-2. Dry mass (W, mg, 60°C, 48 h) of arthropods was estimated from the body length (L, mm) with the following equation: $W = 0.12 L^{1.64}$ ($r = 0.83$, $P < 0.001$, $N = 78$), which was determined based on part of the samples. Leaf areas were measured (using a digitizer) for 25 leaves for each tree species in July to calculate the arthropod dry mass per 1 m² leaf area.

4) Statistical analyses

Chi-square tests were conducted to reveal differences in tree species use among bird species during each research period. Some tree species were combined to make expected frequencies large enough for chi-square tests. Chi-square tests and Fisher's exact probability tests with multiple comparison methods were conducted to compare the frequencies of the tree species used by a bird species with the frequencies expected from tree species composition during each research period. Chi-square tests with multiple comparison methods were also conducted to reveal the differences in foraging techniques used by each bird species between tree species. Mantel-Haenszel tests were conducted to detect similarities of relative frequencies of foraging techniques on different tree species among bird species. The arthropod dry mass

per 1 m²-leaf area data were log-transformed to reduce skewness for ANOVA. Two-way ANOVAs were conducted to reveal the seasonal changes in arthropod abundances on different tree species (factor=period, tree species). One-way ANOVAs were conducted to reveal the differences in arthropod abundances among tree species during each period (factor=tree species). Spearman's rank correlation tests were conducted to reveal the relationship between arthropod abundances and selectivity of tree species for each bird species during each research period. Sequential Bonferroni methods (Rice 1989) were used for multiple comparisons in nonparametric tests and Fisher's PLSDs were used in ANOVA. Statistical significances were evaluated at $P < 0.05$ except for correlation analyses. $P < 0.1$ was considered as the significance level for correlation analyses owing to the small sample sizes involved (4 or 6).

RESULTS

1) Tree species preferences of foraging birds

The uses of tree species differed significantly among bird species during all research periods (Table 1). In the 92-1 period, *A. mono* was preferred by three species of tits and *Q. mongolica* was preferred by Great Tit, but *B. platyphylla* was avoided by most species of birds. In the 92-2 period, neither preference nor avoidance for tree species was shown by any bird species except for Eastern Crowned Leaf Warbler preferring *Q. mongolica*. In the 92-3 period, *K. pictus* was preferred by Marsh Tit and Eastern Crowned Leaf Warbler, but *B. platyphylla* was avoided by Marsh Tit and Japanese White-eye. In the 93-1 period, *A. mono* was preferred by three species of tits and *Q. mongolica* was preferred by Eastern Crowned Leaf Warbler, Japanese White-eye and Narcissus Flycatcher, but *B. platyphylla* was avoided by all species of birds. In the 93-2 period, *B. platyphylla* was avoided by Great Tit and Narcissus Flycatcher. On the whole, the preferred or avoided tree species appeared to be consistent for each bird species during each research period, although the use of tree species differed significantly among bird species (Table 1).

The tree preference index for each bird species was compared between the first (92-1, 93-1) and the later research periods (92-2, 92-3, 93-2). This index decreased for Long-tailed, Great, and Marsh tits, but increased or remained unchanged for the Narcissus Flycatcher in both years (Table 2). This index increased for Eastern Crowned Leaf Warbler in 1992 but de-

Table 1. Preferential use of tree species by foraging bird species and tree species composition in the study area. + or - represent differences between the percent of each bird species using a tree species and the percent of the tree species composition of the same tree species. Some bird species were not shown in each period owing to sample size being too small for analysis. AM=*Acer mono*, AH=*Alnus hirsuta*, QM=*Quercus mongolica*, TJ=*Tilia japonica*, BP=*Betula platyphylla*, KP=*Kalopanax pictus*.

	Tree species						Number of observations	** χ^2 test
	AM	AH	QM	TJ	BP	KP		
92-1 period								
Long-tailed Tit	+22.1*	+4.1	+8.3	+1.8	-32.6*	-4.9	59	$\chi^2=59.0$
Great Tit	+25.8*	-2.9	+16.6*	-0.1	-27.2*	-5.1	142	df ¹⁾ =20
Marsh Tit	+8.5*	+1.6	+9.7	-1.3	-25.0*	-5.1	186	P<0.001
Eastern Crowned Leaf Warbler	+6.5	-0.5	+20.9	-3.1	-9.7	-6.2	52	
Narcissus Flycatcher	+6.7	+2.2	+16.2	-3.7	-22.8*	+1.7	77	
92-2 period								
Long-tailed Ti	+4.5	+5.2	+19.6	-5.0	-22.4	-10.0	21	$\chi^2=33.8$
Great Tit	+9.6	+3.5	-0.3	-3.1	-9.3	-4.2	103	df ²⁾ =12
Marsh Tit	-3.4	-1.0	-2.2	-3.4	-6.3	-8.4	61	P<0.001
Eastern Crowned Leaf Warbler	+2.5	-4.3	+26.3*	-2.5	-21.2	+2.5	40	
Narcissus Flycatcher	+7.9	+2.2	+18.6	+1.5	-29.7	-3.5	31	
92-3 period								
Long-tailed Tit	-5.0	-0.9	+7.0	+1.9	-8.9	-10.0	29	$\chi^2=55.1$
Great Tit	+0.3	+2.7	-0.5	-3.2	-13.7	+11.1	114	df ³⁾ =15
Marsh Tit	-4.1	+2.1	+2.8	-3.2	-14.1	+20.3*	109	P<0.001
Eastern Crowned Leaf Warbler	-1.6	+6.0	-3.4	-5.0	-37.6*	+26.2*	58	
Japanese White-eye	-5.0	+2.8	+22.0	+2.1	-42.6*	+18.5	28	
Narcissus Flycatcher	+11.0	+3.7	+14.3	-1.0	-30.2	+10.0	25	
93-1 period								
Long-tailed Tit	+28.3*	-4.3	+19.6	+1.1	-34.1*	-10.0	33	$\chi^2=55.8$
Great Tit	+18.3*	+1.9	+9.6	+4.6	-29.8*	-5.2	146	df ⁴⁾ =24
Marsh Tit	+17.8*	-2.4	+1.7	+6.1	-24.6*	-8.1*	162	P<0.001
Eastern Crowned Leaf Warbler	+10.1	-0.5	+25.9*	+2.5	-29.2*	-8.1	53	
Japanese White-eye	+11.7	-0.6	+34.4*	-1.3	-42.5*	-10.0	27	
Narcissus Flycatcher	-0.2	-0.7	+28.0*	+3.3	-33.1*	+6.7	84	
Brown Flycatcher	+10.4	-4.3	+20.9	-1.2	-15.4	+1.5	26	
93-2 period								
Great Tit	+9.3	+1.0	+5.1	+7.0	-16.1*	-1.0	133	$\chi^2=26.5$
Marsh Tit	+5.1	-1.8	+8.1	-1.6	-8.4	-3.3	119	df ⁵⁾ =12
Eastern Crowned Leaf Warbler	+2.3	+0.6	+15.5	-0.1	-9.6	-2.7	41	P<0.001
Narcissus Flycatcher	+12.9	+11.1	+11.9	+2.7	-41.1*	+0.2	39	
Tree species composition (%)	5.0	4.3	13.7	5.0	46.2	10.0		

* P<0.05, comparisons of the tree species composition for each tree species and the use of same tree species for each bird species by each period and bird species (χ^2 test or Fisher's exact test with sequential Bonferroni method).

** Comparisons with use of tree species at each period.

1-5) Tree species categories were combined to make expected frequencies large enough for chi-square tests.

1) Six tree categories; AM, QM, TJ, BP, KP, AH+other tree species.

2) Four tree categories; AM, QM, BP, AH+KP+TJ+other tree species.

3) Four tree categories; QM, BP, KP, AM+AH+TJ+other tree species.

4) Five tree categories; AM, QM, TJ, BP, AH+KP+other tree species.

5) Five tree categories; AM, QM, TJ, BP, AH+KP+other tree species.

Table 2. Tree Preference Index during each period. Some bird species were not shown for each period owing to sample sizes being too small for analysis.

	Period				
	92-1	92-2	92-3	93-1	93-2
Long-tailed Tit	73.8	66.7	33.7	97.4	
Great Tit	77.7	30.0	31.5	69.4	39.5
Marsh Tit	51.0	24.7	46.6	60.7	28.3
Eastern Crowned Leaf Warbler	46.9	59.3	79.8	76.3	30.8
Japanese White-eye			93.0	100.5	
Narcissus Flycatcher	53.3	63.4	70.2	72.0	79.9
Brown Flycatcher				53.7	

creased in 1993.

In the first research periods of both years, the uses of tree species were similar among bird species and differed from the tree species composition in the study plot (Fig. 1). In the later research periods, bird species were divided into two groups: the first consisted of bird species that used trees in relation to the tree species composition of the area, while the second consisted of bird species that foraged in trees unrelated to their species composition (Fig. 1). Two *Parus* species usually belonged to the first group, while Narcissus Flycatcher and Japanese White-eye usually belonged to the second group. Long-tailed Tit and Eastern Crowned Leaf Warbler were classified into different groups in different research periods.

2) Foraging techniques on each tree species

Long-tailed Tit used all three foraging techniques with almost the same frequency (Table 3). Great Tit and Marsh Tit foraged by perch-gleaning most frequently but also hang-gleaned (30%). Eastern Crowned Leaf Warbler foraged by hovering most frequently, but also perch-gleaned (30%). Japanese White-eye almost always foraged by perch-gleaning, and Narcissus Flycatcher and Brown Flycatcher almost always foraged by hovering. The variety of foraging techniques was maximal for the Long-tailed Tit, intermediate for the two *Parus* species, Eastern Crowned Leaf Warbler, and Japanese White-eye, and lowest for the two flycatcher species.

Foraging techniques used by each bird species were compared among tree species (Table 4). Significantly different frequencies of gleaning (perch-gleaning + hang-gleaning) and hovering among tree species were found in Long-tailed Tit ($\chi^2=6.20$, $df=2$, $P=0.045$), Great Tit ($\chi^2=15.79$, $df=4$, $P=0.003$) and

Eastern Crowned Leaf Warbler ($\chi^2=16.92$, $df=4$, $P=0.002$). Long-tailed Tit hovered more frequently on *B. platyphylla* than on *A. mono* ($\chi^2=6.24$, $df=1$, $P<0.05$). Great Tit hovered more frequently on *B. platyphylla* than on *A. mono* and *Q. mongolica* (BP vs. AM: $\chi^2=11.13$, $df=1$, $P<0.001$; BP vs. QM: $\chi^2=9.48$, $df=1$, $P<0.05$). Eastern Crowned Leaf Warbler hovered more frequently on *B. platyphylla* than on *Q. mongolica* ($\chi^2=15.66$, $df=1$, $P<0.001$). In all seven bird species, on the whole, hovering on *B. platyphylla* was more frequent than on *A. mono* or *Q. mongolica* (Mantel-Haenszel test with sequential Bonferroni method, BP vs. AM: $\chi^2=13.91$, $df=1$, $P<0.01$; BP vs. QM $\chi^2=36.57$, $df=1$, $P<0.001$).

Moreover, significantly different frequencies of perch- and hang-gleaning among tree species were found in Great Tit ($\chi^2=15.83$, $df=4$, $P=0.003$) and Marsh Tit ($\chi^2=36.91$, $df=4$, $P<0.001$). Both tits foraged by hanging more frequently on *A. mono* and *T. japonica* than on *Q. mongolica* (Great Tit: AM vs. QM: $\chi^2=8.61$, $df=1$, $P<0.05$; QM vs. TJ: $\chi^2=8.98$, $df=1$, $P<0.05$; Marsh Tit: AM vs. QM: $\chi^2=17.96$, $df=1$, $P<0.001$; QM vs. TJ: $\chi^2=7.99$, $df=1$, $P<0.05$). Marsh Tit also hang-gleaned more frequently on *T. japonica* than on *B. platyphylla* ($\chi^2=7.99$, $df=1$, $P<0.05$). In the four gleaning species (Long-tailed Tit, *Parus* species, and Japanese White-eye), hang-gleaning on *A. mono* was more frequent than on *Q. mongolica* or *B. platyphylla* (Mantel-Haenszel test with sequential Bonferroni method, AM vs. QM: $\chi^2=16.02$, $df=1$, $P<0.001$; AM vs. BP: $\chi^2=10.86$, $df=1$, $P<0.01$), and hang-gleaning on *T. japonica* was more frequent than on *Q. mongolica*, *B. platyphylla* or *K. pictus* (TJ vs. QM: $\chi^2=31.75$, $df=1$, $P<0.001$; TJ vs. BP: $\chi^2=14.00$, $df=1$, $P<0.01$; TJ vs. KP: $\chi^2=8.07$, $df=1$, $P<0.05$).

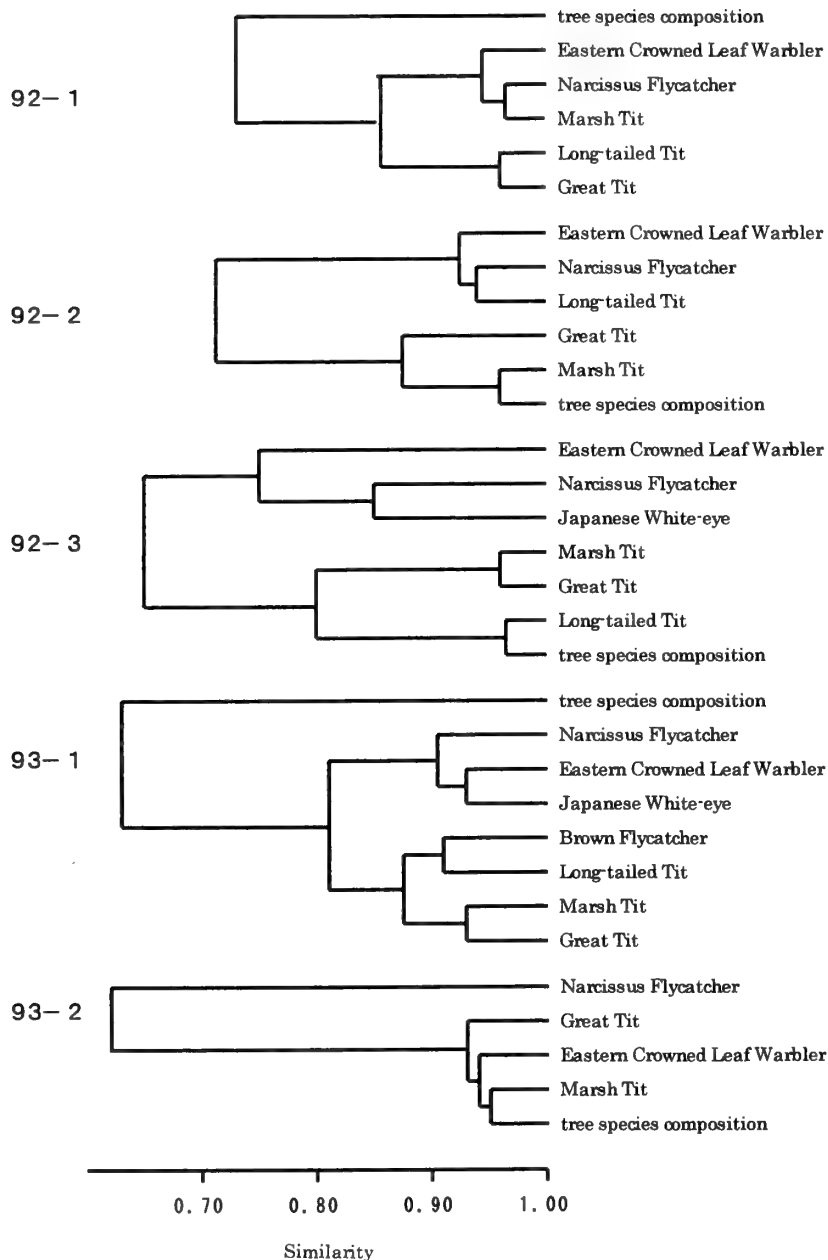


Fig. 1. Similarity between use of tree species by bird species and the tree species composition shown by means of α index (Pianka 1973). Dendrograms were constructed according to Mountford (1962).

These four bird species, Long-tailed tit, *Parus* species, and Eastern Crowned Leaf Warbler, which changed their foraging techniques between different tree species, used the widest range of foraging techniques (Table 3).

3) Prey abundances on each tree species

Arthropod abundances (dry mass/1 m² leaf surface area) changed seasonally, with the fluctuation patterns differing among tree species in each year (Fig.

2, two-way ANOVA, 1992: periods, $F_{83,2}=4.78$, $P=0.011$; tree species, $F_{83,3}=1.64$, $P=0.19$; periods \times tree species, $F_{83,6}=2.45$, $P=0.033$; 1993: periods, $F_{113,1}=8.86$, $P=0.004$; tree species, $F_{113,5}=8.02$, $P<0.0001$; periods \times tree species, $F_{113,5}=1.13$, $P=0.35$). Arthropod abundances differed among tree species in 92-1, 93-1, and 93-2 but not in 92-2, or 92-3 (one-way ANOVA; 92-1: $F_{27,3}=5.26$, $P=0.006$; 92-2: $F_{27,3}=1.88$, $P=0.16$; 92-3: $F_{27,3}=0.62$, $P=0.61$, 93-1: $F_{59,5}=4.63$, $P=0.002$; 93-2: $F_{53,5}=4.51$, $P=0.002$).

Tree Species Preferences of Birds

Table 3. Bird foraging techniques.

	Gleaning (%)		Hovering (%)	Diversity index Shannon's H'	Number of observation
	Perch-gleaning	Hang-gleaning			
Long-tailed Tit	25.7	45.5	28.8	1.54	132
Great Tit	60.0	32.3	7.7	1.25	637
Marsh Tit	59.7	33.3	7.0	1.24	1079
Eastern Crowned Leaf Warbler	28.5	4.7	66.8	1.11	240
Japanese White-eye	80.2	17.0	2.8	0.83	274
Narcissus Flycatcher	7.5	1.7	90.8	0.51	106
Brown Flycatcher	10.7	0.0	89.3	0.49	56

Table 4. Foraging techniques on each tree species. Parentheses show the number of observations. Because of small sample sizes comparison of Long-tailed Tit, Brown Flycatcher, and Japanese White-eye's foraging techniques on Caster arealia and Japanese linden were omitted (see Table 1 for AM, AH, QM, TJ, BP, and KP).

	Gleaning (%)	Hovering (%)		Gleaning			
				Perch-gleaning (%)	Hang-gleaning (%)		
Long-tailed Tit							
AM	83.7 (36)	16.3 (7)	↑ *	37.2 (9)	62.8 (27)		
QM	70.6 (24)	28.4 (10)	↓	58.8 (10)	41.2 (14)		
BP	56.0 (14)	44.0 (11)		68.0 (6)	32.0 (8)		
Great Tit							
AM	94.6 (194)	5.4 (11)	↑ **	63.9 (120)	36.1 (74)	↑ *	
QM	94.7 (144)	5.3 (8)	↓ *	78.3 (111)	21.7 (33)		↑ *
TJ	86.5 (32)	13.5 (5)	↓	54.0 (15)	46.0 (17)		↓
BP	82.8 (82)	17.2 (17)		75.8 (58)	24.2 (24)		
KP	92.3 (36)	7.7 (3)		64.1 (22)	35.9 (14)		
Marsh Tit							
AM	90.5 (134)	9.7 (14)		56.7 (70)	43.3 (64)	↑ **	
QM	95.8 (256)	4.2 (8)		78.4 (199)	21.6 (57)	↓	↑ **
TJ	78.4 (34)	21.6 (3)		45.9 (14)	54.1 (20)	↑ **	↓
BP	92.1 (232)	7.9 (20)		69.4 (155)	30.6 (77)	↓	
KP	95.2 (80)	4.8 (4)		70.0 (55)	30.0 (25)		
Eastern Crowned Leaf Warbler							
AM	35.0 (7)	65.0 (13)		95.0 (6)	5.0 (1)		
QM	44.1 (49)	55.9 (62)	↑ **	97.3 (46)	2.7 (3)		
TJ	25.0 (4)	75.0 (12)		100.0 (4)	0.0 (0)		
BP	5.7 (11)	84.3 (59)	↓	95.7 (8)	4.3 (3)		
KP	23.1 (3)	76.9 (10)		92.3 (2)	7.7 (1)		
Japanese White-eye							
AM	96.0 (24)	4.0 (1)		76.0 (18)	24.0 (6)		
QM	100.0 (51)	0.0 (0)		90.2 (46)	9.8 (5)		
BP	66.7 (2)	33.3 (1)		100.0 (2)	0.0 (0)		
Narcissus Flycatcher							
AM	10.3 (3)	89.7 (26)		100.0 (3)	0.0 (0)		
QM	11.1 (9)	88.9 (72)		98.8 (8)	1.2 (0)		
TJ	6.7 (1)	93.3 (14)		100.0 (1)	0.0 (0)		
BP	4.6 (2)	95.4 (42)		100.0 (2)	0.0 (0)		
KP	5.7 (2)	94.3 (33)		97.3 (1)	2.7 (1)		
Brown Flycatcher							
AM	15.4 (2)	84.6 (11)		100.0 (2)	0.0 (0)		
QM	19.1 (3)	80.9 (17)		100.0 (3)	0.0 (0)		
BP	0.0 (0)	100.0 (18)		100.0 (0)	0.0 (0)		

*: $P < 0.05$, **: $P < 0.01$.

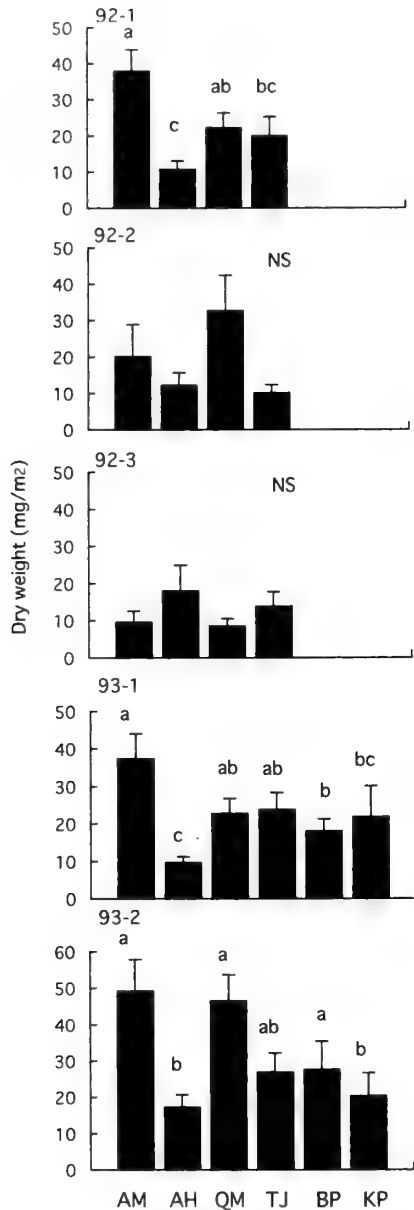


Fig. 2. Arthropod dry mass per 1 m² leaf area on various tree species (mean \pm SE). Refer to Table for AM, AH, QM, TJ, BP, and KP. BP and KP were not surveyed in 1992. Letters above vertical lines indicate the results of multiple comparison tests (Fisher's PLSD, $P < 0.05$); the same letters indicate non-significant differences.

In the first research periods of each year, arthropod abundances were highest in *A. mono* (Fig. 2).

Of the 27 cases of correlation analyses for each bird species during each research period, there were seven positive relationships (26%) between selectivity by birds and arthropod abundance on different tree species (Table 5). Of the seven significant relationships, six (86%) were found for the four bird species,

Long-tailed tit, *Parus* species, and Eastern Crowned Leaf Warbler, using wide range of foraging techniques (Table 3) and five (71%) were found during the first research periods.

DISCUSSION

Tree species supporting high prey abundance can be expected to be preferred by foraging birds (Hino et al. 2002). Prey abundance may explain why *A. mono* was most preferred by tit species during the first research periods each year. In most cases, however, tree species preferences were not related to prey abundances on trees. Some researchers have indicated that tree species preferences of birds are influenced not only by food abundance but also by food accessibility, that is foliage structure of trees and manoeuvrability of birds both play a role (Holmes & Robinson 1981; Whelan 1989; Dias et al. 1998). For example, *Q. mongolica* was preferred but *B. platyphylla* was avoided by most bird species despite them supporting similar abundances of prey. This result may be attributable to the different accessibility of food in relation the foliage structure of these tree species. Almost all birds captured prey by hovering on *B. platyphylla* more frequently than on *Q. mongolica*. *B. platyphylla* has fine twigs, long petioles, and horizontally distributed leaves, which make searching and capturing prey while perching difficult, and make sallying or hanging from branches necessary. In contrast, *Q. mongolica*, which has thick twigs, very short petioles and a more three-dimensional distribution of leaves, provides more opportunities for foraging by perch-gleaning. Because perch-gleaning is a less energy-expensive foraging technique than hang-gleaning and hovering, capturing prey on *Q. mongolica* is less energy-expensive for birds than taking the same prey from *B. platyphylla*. Thus, birds should prefer *Q. mongolica* rather than *B. platyphylla*. Likewise, the food accessibility for gleaner species (Long tailed Tit, *Parus* species, and Japanese White-eye) may be influenced by the foliage structure of *A. mono* and *T. japonica*. These birds foraged frequently by hanging from twigs on these trees. Because leaves are distant from twigs, owing to the upward pointing long petioles of these trees, hang-gleaning would be an efficient technique to capture prey from the undersides of leaves where most caterpillars are found (Greenberg & Gradwohl 1980; Holmes & Schulz 1988).

The present results supported my hypothesis that there is a correlation between the variety of foraging

Table 5. Results of correlation analyses between Ivlev's electivity index of foraging bird species and arthropod abundances on each tree species. Spearman's rank correlation tests were one-tailed. Because of a few observations, results of Long-tailed Tit in 93-2, Japanese White-eye in 92-1, 92-2 and 93-2, and Brown Flycatcher in 92-1, 92-2, 92-3, and 93-2 were omitted.

	Periods (Number of tree species)				
	92-1 (4)	92-2 (4)	92-3 (4)	93-1 (6)	93-2 (6)
Long-tailed Tit	NS	NS	NS	(+)	
Great Tit	+	NS	NS	++	NS
Marsh Tit	NS	NS	NS	(+)	++
Eastern Crowned Leaf Warbler	NS	+	NS	NS	NS
Japanese White-eye			NS	NS	
Narcissus Flycatcher	NS	NS	NS	(+)	NS
Brown Flycatcher				NS	

Positive correlation: ++; $P < 0.01$, +; $P < 0.05$, (+); $0.1 < P < 0.05$.

techniques a bird uses and its flexibility of response to spatio-temporal changes in food resources. Bird species employing a wide range of foraging techniques, Long-tailed Tit, *Parus* species, and Eastern Crowned Leaf Warbler, changed their foraging techniques among different tree species. This must be an effective foraging tactic because the most efficient technique will depend on foliage structure. In contrast, birds with specialized foraging techniques did not show such a flexible response among tree species. The tree species that such specialists can forage from efficiently must be constrained by foliage structure. Japanese White-eye, a perch-gleaning specialist, would find it difficult to capture prey on trees with leaves distant from twigs, from which they cannot reach the leaves, or on trees with fine twigs where they cannot perch. Flycatchers, hovering specialists, are unlikely to be able to capture prey inhabiting rolled leaves because they cannot open such leaves or insert their bills into such leaves while holding branches or leaves (Murakami 1999).

The foraging techniques used were also related to a bird's response to seasonal changes in food resources. In the first research periods each year, birds resembled one another in their use of tree species, and their use differed considerably from the natural tree species composition. That is, all seven bird species were actively selecting the same particular tree species. In the later research periods, however, two different responses were found among bird species. Bird species with a wide range of foraging techniques (Long-tailed Tit and *Parus* species) changed and became non-selective, while those with specialized techniques (Japanese White-eye and flycatcher species) remained selective. In the late periods, East-

ern Crowned Leaf Warbler was selective in 1992 but not selective in 1993. This yearly change may be attributable to this species' intermediate range of foraging techniques. Contrary to expectation, Long-tailed Tit, which has the widest range of foraging techniques, remained selective in 1992, although thus difficult to interpret result may have been because of the small sample size ($N=21$).

Why did birds using a wide range of foraging techniques become generalized in selecting tree species in later seasons? MacArthur (1972) predicted that foragers should be more specialized in productive than in unproductive environments. The same prediction was also given by the average-rate maximizing model combining the prey and patch models (Stephens & Krebs 1986). The present study showed that either prey abundance did not change, or it increased in later seasons. I expect, however, that a birds' requirement for prey is higher during the later research periods (early June to early July) owing to the addition of nestlings and fledglings. Accordingly, the non-selective use of tree species by bird species with a wide range of foraging techniques may have been an appropriate response to the seasonal change in prey abundance.

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SHORT COMMUNICATION

Bird predation by domestic cats on Hahajima Island, Bonin Islands, Japan

ORNITHOLOGICAL
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The Bonin Islands are oceanic islands situated in the northwest Pacific Ocean 1,000 km south of the Japanese main island of Honshu. These islands lacked terrestrial mammalian carnivores until human colonization in 1830. Early immigrants introduced domestic cats *Felis catus* to the islands, some of which escaped from the island's residential area. Even by 1877 there were already reports of there being many feral cats on the island (Obana 1877). Cat predation is known to impact native bird populations on various islands around the world, such as the offshore islands of New Zealand and the Canary Islands in the eastern Atlantic Ocean (Fitzgerald & Veitch 1985, Nogales et al. 1992, Powlesland et al. 1995). In the Bonin Islands also, many studies have highlighted the impact of cat predation on native birds (e.g. Tokyo Regional Forest Office 1994, Tokyo Regional Forest Office 1996, Kawakami 2000). Yamashita (1934) supposed that the extinction of endemic birds (such as the Ogasawara Islands Thrush *Turdus terrestris* and the Ogasawara Islands Grosbeak *Chaunoproctus ferreorostris*) in the Bonin Islands was partly caused by predation of increased feral cats. But, no detailed study has been conducted on the diet of feral cats. Cat predation on small birds is considered to be underestimated, because such prey are eaten whole by cats and few visible remains are left after predation (Kawakami 2000).

In order to elucidate the extent of predation on native Bonin Island passerines, we collected, and identified, the feathers of birds eaten by a domestic cat. The cat involved was a free-roaming neutered tabby female about eight years old. The cat brought prey remains, including feathers, to the cat-owner's house in the Okimura area of Hahajima (Haha Island). The

owner collected feathers, at our request, whenever he found them. The collection was conducted from September 1998 to November 1999. The owner was not absent for any prolonged periods during the survey, nor was the collection effort biased seasonally. The remains included not only feathers but also a few torn legs, wings and heads, which were available for species identification. We referred to feather specimens, photos and measurement data to identify the feathers. As the samples included characteristic pieces of various body parts, we were easily able to identify the species concerned. The minimum number of each species estimated from feather samples was recorded. English names and classification follow the Ornithological Society of Japan (2000).

The feathers were identified as belonging to 39 individuals of four species: thirty-one Japanese White-eyes *Zosterops japonicus*, five Bonin Islands Honeyeaters *Apalopteron familiare*, two Siberian Meadow Buntings *Emberiza cioides*, and one Oriental Greenfinch *Carduelis sinica*. The number predated was particularly high during the breeding season probably because of the greater vulnerability of fledglings. Though Brown-eared Bulbuls *Hypsipetes amaurotis* and Blue Rock Thrushes *Monticola solitarius* also occurred on the island they were not found among the remains. As these species are larger than the other four species, the cat may either prey on them less frequently than the other species, or did not bring them to the house. Kawakami (2000) reported that these species and other larger birds were preyed upon by cats. Therefore, it is considered that bulbuls and rock-thrushes are within the normal prey range, but for some reason were not recorded in this survey. The white-eye is an introduced species, now the dominant species in the study area. The honeyeater is endemic to the islands and is classed as a vulnerable species by Birdlife International (2001). The sub-

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species of the greenfinch on the Bonin Islands, *C. s. kittlitzi*, is endemic to the islands and its population is considered to be at most 200 individuals (Tokyo Regional Forest Office 1996). These three species are residents, whereas the bunting is a winter visitor to the islands.

On Hahajima, feral cats have been observed widely in various kinds of habitats, including primary forests. There is no appropriate estimate of their population, however judging by the frequency of detection, there are likely to be more than 100 feral or half-feral cats on the island. The cat we studied was a free-roaming domestic individual fed regularly by its owner, thus its hunting was supplementary to its basic dietary needs. Feral cats are presumed to prey on even more birds. We are unable to estimate the frequency of predation on birds by the study cat, because it did not bring all its prey to the house.

The Japanese White-eye is the dominant species in the study area and was the commonest species represented among the prey remains, indicating that the cat took them in proportion to their availability. As the population density of this species has increased over the last 20 years (Kawakami, K. unpublished data), the impact of cat predation on it is not deemed critical. Predation by cats is a serious problem, however, for the two endangered native passerines—the endemic Bonin Islands Honeyeater, and the endemic subspecies of the Oriental Greenfinch. Since both of these species frequently forage on the ground, they make easy prey for cats. As the total number of the latter is particularly small, the urgent eradication of feral cats is essential as a conservation measure.

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SHORT COMMUNICATION

Gape patches in Oriental Cuckoo *Cuculus saturatus* nestlingsORNITHOLOGICAL
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In areas where more than one brood parasitic *Cuculus* species occurs, identification of their eggs and nestlings is a problem for ornithologists (Payne 1997). The situation is complex in Japan where four *Cuculus* species, the Common Cuckoo *C. canorus*, the Oriental Cuckoo *C. saturatus*, the Little Cuckoo *C. poliocephalus*, and the Horsfield's Hawk Cuckoo *C. fugax* breed largely sympatrically. Although they differ in major host species and usually lay eggs more or less mimetic to their hosts', different cuckoos have occasionally been found to use the same host species, and host usage may change with time (Brooke & Davies 1987; Nakamura 1990; Higuchi 1998).

The Oriental Cuckoo is an example of such a complex situation. In most parts of Japan, Oriental Cuckoos normally lay buff-coloured eggs into *Phylloscopus* Warblers' nests, while Little Cuckoos parasitize the Bush Warbler *Cettia diphone* and lay mimetic reddish eggs. In central Hokkaido (northernmost main island of Japan), however, where the Little Cuckoo is absent, Oriental Cuckoos have been reported to parasitize Bush Warblers and lay reddish eggs (Higuchi & Sato 1984). In this case, "mystery" nestlings were taken from Bush Warbler nests in Hokkaido and reared by hand to a size at which they could be identified.

We were able to observe an Oriental Cuckoo nestling and found that it had prominent black gape patches. In this paper we describe the gape patches and discuss their reliability for species identification of *Cuculus* nestlings in Japan.

MATERIALS

On 19 May 2000, we found a nest of the Eastern

Crowned Leaf Warbler *Phylloscopus coronatus* in a deciduous forest on Mt. Tsukuba (877 m, 36°13'N, 140°06'E), central Japan, containing five small white eggs and one larger buff egg. Although the buff-coloured egg had many brown spots overall, these were concentrated, forming a broad band between the obtuse end and the broadest part of the egg (Fig. 1), characters common in Oriental Cuckoo eggs from central Japan (Kiyosu 1978). The egg size (21.3 × 14.0 mm) was also within the range of the Oriental Cuckoo (19.1–21.5 × 13.7–15.2 mm, Kiyosu 1978).

At 1600 on 26 May, we found that a nestling occupied the nest, and three white eggs and a small dead nestling were found outside of the nest. The nestling in the nest could not have been more than 3 days and 7 hours old at this time, as it had not yet hatched when we checked the eggs in the nest at 0900 on 23 May. On 8 June, after we measured and ringed the nestling, it left the nest and moved into a bush several meters away from the nest. The nestling was not observed after that.

All four Japanese *Cuculus* species occur on Mt. Tsukuba. While Oriental and Little Cuckoos are common summer visitors, Common and Horsfield's Hawk Cuckoos are rare and were not observed in 2000. The nestling's plumages on head, back, scapulars and breast were slaty-black, these feathers faintly fringed with white, and much darker than in the Common Cuckoo (Higuchi & Sato 1984). The belly and flanks were dark blackish brown with obscure white bands, not white with blackish bands as in Little Cuckoo nestlings (Higuchi & Payne 1986) nor white with fine streaks as in Horsfield's Hawk Cuckoo nestlings (e.g. Nakamura & Nakamura 1995, p 110; Kiyosu 1978, p 40; Yoshino 1999, pp 61–63). The nestling's tarsus length reached 21.2 mm and exceeded the range found in adult Little Cuckoos (16–19 mm, Kiyosu 1978). We therefore concluded that

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the nestling was an Oriental Cuckoo, which is consistent with what was indicated by the host species and the egg morphology.

RESULTS

The nestling had remarkable blackish gape patches when it was first observed (Fig. 2a) and it kept them until leaving the nest (Fig. 2b, 2c). Two triangular patches on the palate adjoin the cutting edges of the upper mandible (Fig. 2b). Another pair of patches on the inside of the lower mandible was smaller and more rounded (Fig. 2c).

We also found similar gape patches in a photograph of a fledgling from a northern population of the Oriental Cuckoo (Fig. 3). The bird was taken from a Bush Warbler nest in central Hokkaido, and reared by hand (Higuchi & Sato 1984, for detail). Thus, the gape patches were present in two birds from different Japanese "gentes", one parasitizing *Phylloscopus* Warblers with buff-coloured eggs and the other one parasitizing Bush Warblers with reddish eggs.

There are few published photographs of Oriental Cuckoo nestlings or fledglings in Japan. A naked nestling that occupied the nest of the Bull-headed Shrike *Lanius bucephalus* (Nakamura & Nakamura 1995, p 110, no information for location), unfortunately closed its bill and did not show its gape. A photograph of a fledgling being fed by an Eastern Crowned Leaf Warbler at the foot of Mt. Fuji, central Japan (Kiyosu 1966, p 122), was taken from the side and so that the gape is not visible. For areas outside Japan, a photograph of a nestling being fed by *Phylloscopus tenellipes* in the Russian Far East (Payne 1997, p 536) showed apparent gape patches as in the Japanese birds. A nestling being fed by an Eastern Crowned Leaf Warbler in Ussuriland (Knystautas 1993, plate 43; Campbell & Lack 1985, p 68, apparently the same nestling) is of a bird with its head turned away and hardly showing the gape. In a photograph taken in Malaysia (Becking 1975), a fledgling *C. saturatus lepidus* fed by a Chestnut-crowned Warbler *Seicercus castaniceps* seems to have gape patches, but it is too dark to allow further comments.

We could find only few descriptions of the Oriental Cuckoo's gape. Payne (1997, p 555) noted that "Nestling naked at hatching, orange gape, black gape flanges" in Horsfield's Cuckoo (*Cuculus horsfieldi*, which he recognized as a species distinct from other races of Oriental Cuckoo based on differences in song and morphological traits). Payne (1997) may

refer to the black gape patches we have described here, although the gape flanges were mostly orange in the birds that we examined.

DISCUSSION

The Oriental Cuckoo has four subspecies, *C. s. horsfieldi*, *C. s. saturatus*, *C. s. lepidus* and *C. s. insulindae* (Becking 1975; Wells & Becking 1975; Cramp 1985) and all three birds recorded as showing gape patches belonged to *C. s. horsfieldi*, which is the northernmost breeder of the four and is wholly migratory. Our results, therefore, suggest that Oriental Cuckoo nestlings and fledglings, at least within the subspecies *C. s. horsfieldi*, have black gape patches, independent of egg types and region. Presence of gape patches, thus, should be a key character to identify young Oriental Cuckoos because they seem to be unique to this species. The Common cuckoo has not been described as having gape patches, despite the species having been the subject of extensive studies in Europe and Japan, including of the gape area and colour of nestlings (e.g., Kilner et al. 1999; Noble et al. 1999). Two Little Cuckoo nestlings that we found on Mt. Tsukuba in 2000 both lacked gape patches (Fig. 4), as did those in various published photographs (e.g., Nakamura & Nakamura 1995, p 109; Yoshino 1999, p 56). Horsfield's Hawk Cuckoo nestlings, unlike other Japanese *Cuculus* species, have yellow gapes without black patches (Kiyosu 1978, p 40; Yoshino 1999, p 61). Therefore, if one finds a naked *Cuculus* nestling with gape patches in Japan, it is most likely to be an Oriental Cuckoo. This is a very useful identification feature because nest predation is often so frequent that the nestlings disappear before other morphological characteristics become visible. Taking and rearing nestlings by hand, as well as blood sampling requires governmental permission. In most cases when *Cuculus* eggs or nestlings are found unintentionally, it would be impossible to obtain the necessary permission before they fledge.

It should be noted that even a nestling without gape patches might be an Oriental Cuckoo. The gape patches appeared within about three days from hatching, but we do not know exactly when. Therefore, very small Oriental Cuckoo nestlings, possibly during the first or second day, may not have gape patches. Gape patches in such small nestlings, as well as those in other subspecies of this species, need further investigation.



Fig. 1. An egg of Oriental Cuckoo (the largest one) and five eggs of its host, an Eastern Crowned Leaf Warbler. 19 May 2000 on Mt. Tsukuba, Central Japan.



Fig. 2c. The same Oriental Cuckoo nestling as in Fig. 2b, showing a pair of patches on the inside of the lower mandible. 8 June 2000.



Fig. 2a. An Oriental Cuckoo nestling hatched from the egg in Fig. 1. It was two or three days old and had prominent gape patches at this age. 26 May 2000.



Fig. 3. A 30-days-old Oriental Cuckoo fledgling taken from a Bush Warbler nest in central Hokkaido and reared by hand.



Fig. 2b. The Oriental Cuckoo nestling hatched from the egg in Fig. 1 at 15 or 16 days of age, showing a pair of patches on palate. 8 June 2000.



Fig. 4. A Little Cuckoo nestling at about 14 days of age, showing its gape. It had parasitized a Bush Warbler nest on Mt. Tsukuba. 1 August 2000.

It is not clear whether the gape patches in young Oriental Cuckoos have any adaptive functions. It seems unlikely that the patches mimic corresponding patches in their host species because, as far as we know, none of the host species of the Oriental Cuckoo has such gape patches (e.g., Harrison 1975). Viduine birds which are parasitic on estrildine finches mimic mouth parts of their host's nestlings, as each estrildine host will feed only young with the distinctive mouth parts of its own species (Lack 1968; Nicolai 1974). Host parents of *Cuculus* cuckoos, unlike estrildine finches that rear parasite nestlings alongside their own, generally have difficulties discriminating young cuckoos from their own offspring because the newly hatched cuckoos usually eject all host eggs and nestlings to occupy the nest alone (Payne 1997). Davies and Brooke (1989) found no evidence of chick discrimination in experiments with four major host species of the Common Cuckoo.

Gaping in cuckoos may affect the behaviour of host parents and of predators. Kilner et al. (1999) described how the gape area of Common Cuckoo nestlings shown to host parents, in combination with begging call rate, determined host provisioning rates. Therefore, the gape patches in Oriental cuckoo nestlings may serve to influence parental behaviour, although gape colour had no effect on provisioning rates in three major host species of Common Cuckoos in Britain (Noble et al. 1999). Noble et al. (1999) suggested that the vivid gape colours of Common Cuckoo nestlings might have an aposematic function, as older cuckoo nestlings have a threat display that involves gaping at intruders. The Oriental Cuckoo nestling also threatened observers by gaping and the distinct pattern of the gape patches might provide additional benefits when threatening and attempting to deter certain predators.

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SHORT COMMUNICATION

Common Raven *Corvus corax* at play; records from JapanORNITHOLOGICAL
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of Japan 2002Mark BRAZIL[#]*Environmental Systems Faculty, Rakuno Gakuen University, 582–1 Midorimachi, Bunkyo-dai,
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Play is a notoriously difficult complex of behaviours to define. While many observers recognise play in general, they struggle to define it. Bekoff (1984), in one widely accepted definition described it as "...all motor activity performed postnatally that appears purposeless, in which motor patterns from other contexts may often be used in modified forms or altered sequencing." More succinctly, play is generally interpreted as any behaviour displayed by an animal which does not seem to have any direct adaptive advantage. The animals involved seem to the observer to engage in the behaviour for the fun of it (Heinrich & Smolker 1998). Among the Passeriformes it is the corvids that are considered to exhibit the most complex play behaviour. The Common Raven *Corvus corax* is the largest of the corvids and its tremendous behavioural flexibility may in part be acquired through play (Ficken 1977; Ortega & Bekoff 1987). Various elements of play behaviour have previously been described among ravens including play catching, flight play, bathing play, vocal play, hanging, games, allospecific interactions, sliding and 'snow-romping' (Ratcliffe 1997; Heinrich & Smolker 1998), but no such behaviours seem to have been described from Asia.

The Common Raven is a widespread, mainly sedentary Holarctic, and marginally Neotropical, species. The subspecies *C. c. kamtschaticus* Dybowski, 1883, was previously, and until recently, considered an uncommon, scarce or even rare winter visitor to a very few areas of Hokkaido, Japan, most often in the coldest part of the winter during January and February most notably on the Shiretoko Peninsula, particularly along rocky seacoasts where there are cliffs (OSJ 1974; WBSJ 1982; Yanagisawa 1988; Brazil 1991; Kanouchi & Abe 1998; Iozawa 2000; Onishi 2000; OSJ 2000). Especially during the 1990s, however, the raven has become a locally common

species in certain areas wintering from as early as November until as late as May (Brazil pers. obs.). This subspecies breeds in Siberia, from the Yenisei River and Lake Baikal in the west to the Okhotsk and Pacific coasts of Kamchatka and the Commander Islands in the east, and south as far as Sakhalin and the Kurile Islands. The birds reaching Hokkaido in winter are presumed to be of this subspecies and to migrate from adjacent areas in the Okhotsk Sea region, perhaps from as far away as Kamchatka.

Two areas where Common Ravens may now be found commonly in winter in Japan are the well forested, mountainous, Akan National Park (NP) in central eastern Hokkaido, and the equally mountainous Shiretoko Peninsula of extreme northeast Hokkaido. There, increasing numbers of ravens have facilitated recent behavioural observations (including those of play) that would not have been possible in the past when they were scarcer.

Gwinner (1964) described captive ravens repeatedly sliding down an inclined shiny board, and Ratcliffe (1997) described wild ravens as playing or rolling over in snow 'like a dog.' Ravens have also been observed sliding down steep snow-covered roofs in Alaska and northern Canada (Heinrich & Smolker 1998), sliding on their backs down snow-slopes in Maine, USA, and in Britain (Moffett 1984; Heinrich & Smolker 1998), and as sliding on their breasts in Maine (Heinrich 1990), while Kilham (1989, in Ratcliffe 1997) apparently kept a tame raven that enjoyed sliding on its side and rolling.

Fieldwork in the Akan NP since May 1998 (study in progress) has enabled me to observe a large number of ravens on numerous occasions and exhibiting a wide range of behaviours including communal gatherings, aerial displays, and apparent courtship. A considerable amount of raven flight behaviour appears playful and this can commonly be seen in Hokkaido during winter. On three occasions only, however, have I been fortunate enough to observe ravens in Hokkaido engaging in other forms of what can only

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be described as play behaviour. The most interesting of these involved sliding and rolling in snow—"snow-romping" (Ratcliffe 1997).

OBSERVATIONS

1) Observation one

On the morning of 8 February 2000, in clear sunny conditions ten ravens, apparently four pairs and two singles, as judged from their behaviour and their calls, were engaging in aerial chases, displays, and calling activity, both in the air and from among the rocks on the upper slopes of Atosanupuri (Io-san) and Makuwanchisappu (Kawayu 43°37'N; 144°25'E). At the time the temperature had warmed to approximately -5°C and the ground was covered with fresh powder snow, which was deep on the lower flanks of the mountains.

At approximately 10:45, I located two ravens on a steep slope on the lower eastern flank of Makuwanchisappu where the low Japanese Stone Pine *Pinus pumila* forest was buried in snow leaving an open snow slope. These two individuals were engaged in behaviour I have not observed in Japan before. One of them, after landing in the snow, lay on its breast and slid head forwards downhill in the snow on its breast, apparently 'sledging.' Its partner, nearby, began by lying sideways to the slope and rolled over and over downhill. The pair continued 'sledging' and rolling downhill for more than ten metres before flying back upslope. This they did repeatedly. Less than five minutes later I noticed a second pair also engaged in such apparent play behaviour. One member of this pair was fluttering in deep powder snow as if bathing, while its partner was rolling sideways down the slope nearby in the same way as one of the members of the first pair. As this bird rolled over repeatedly on to its back I was very clearly able to see its legs in the air, its wings flicking in the snow each time, before it rolled over upright again. A third pair nearby was also engaged in similar behaviour; one member was rolling sideways down the slope in the snow when first seen, but was quickly joined by its apparent partner, which landed on it, sat down on it, and remained in that position for at least a minute. Meanwhile one member of the first pair was still sliding headfirst down the slope. The three pairs were engaged almost simultaneously in play behaviour in the snow.

Rolling by the ravens disturbed the powdered snow in an erratic manner; however, 'sledging' left clear

linear tracks in the snow. When I scanned the entire eastern flank of Makuwanchisappu I was able to recognise the distinctive tracks, disturbing the otherwise smooth snow, where ravens had played in more than ten different places indicating that they had been playing for some time before I first noticed them.

2) Observation two

On the afternoon of 9 February 2002, in heavily falling snow, I observed a group of 14 ravens in trees close to a deer carcass near Kanayama Bridge, Shiretoko Peninsula. Amongst the group several pairs were sitting in close proximity to each other (less than one metre apart), one such pair was engaged in allopreening. Meanwhile, at 14:20, a single individual began pecking at the branch it stood on. After a few moments, it slipped into a hanging position beneath the branch, holding on with both feet. While upside down beneath the branch it let go with one foot, holding on with the other. It then grasped the branch in its beak and let go with both feet so that it hung beneath the branch holding on only with its bill. Finally after a few tugging motions, as if attempting to break the branch using its weight, while hanging by its bill, it flew off.

3) Observation Three

On the afternoon of 10 February 2002, in clear bright weather at Mashu-ko, Akan NP, I observed a group of 15 ravens engaged in aerial chases and aerobatics. At 14:19 I noticed one individual landing on the snow slope on the inner rim of the Mashu-ko crater. It proceeded to peck out a large chunk of snow crust (larger than its head), which it picked up in its beak and flew off with. It was immediately chased by another individual, but after circling for approximately one minute it returned to the same part of the slope and dropped the chunk of snow. Approximately five minutes later, another, or the same pair, engaged in the same sequence of behaviours—pecking out snow crust, carrying it into the air, pursuit, then dropping the snow crust back on the slope.

I also observed one pair engaging in an unusually extreme form of aerial play that I have not found described in the literature. Amongst a group of 32 birds, many of which were engaged in aerial pursuits, paired flights, swoops, stalls, and rolling displays, two individuals flew towards each other, grasped each other by their beaks and descended slowly with their wings and tails spread like two black parachutes. After several seconds they disengaged and

flew off separately.

DISCUSSION

Heinrich and Smolker (1998) in their review of play in Common Ravens concluded that because ravens maintain long-term monogamous pair bonds, "successful competition in the mate-choice arena is absolutely critical to lifetime reproduction." Behaviours that appear playful may in fact represent "showing-off" behaviour to other individuals, as status enhancing displays of critical importance in establishing mateships. Heinrich and Smolker (1998) describe various aspects of apparent aerial play that even the most casual observer of ravens is also likely to note. Heinrich and Smolker (1998) also describe ravens hanging upside down from branches, ropes, and power lines, and playing games that involve passing or catching objects in the air.

Although play behaviour, and particularly aerial play, hanging, and 'snow-romping' by ravens, has been described by several authors from Europe and North America (e.g. Gwinner 1964; Moffett 1984; Heinrich 1990; Ratcliffe 1997; Heinrich & Smolker 1998), none of these behaviours appear to have been reported from Japan before. Other species of crows have, however, been observed playing in Japan, in particular the Carrion Crow *Corvus corone*. For example, in the late 1980s Mitsuhiro Kanazawa observed two Carrion Crows sliding on solar panels in Takasaki, Gunma Prefecture. In this case the birds slid standing up with their wings partly spread (Karasawa 1992). Carrion Crows have also been seen and photographed sliding down a children's slide in a park in Shinnanyo-shi, Yamaguchi Prefecture; in this instance standing, and on its side, with its wings closed (Karasawa 1996).

These observations from the Akan NP and the Shiretoko Peninsula, Hokkaido, appear to represent the first time that such play behaviours have been observed among Common Ravens in Asia, and the first time anywhere that pairs have been reported 'sledding' and 'rolling' together, and parachuting together.

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SHORT COMMUNICATION

The first record of cavity nesting in the Ogasawara Islands Honeyeater *Apalopteron familiare* on Hahajima, Bonin Islands, Japan

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The Ogasawara Islands Honeyeater *Apalopteron familiare* is endemic to the Bonin Islands, where it survives only on Hahajima in the southern part of that island group (Ornithological Society of Japan 2000); it is classified as vulnerable by Birdlife International (2000). It typically builds its nests in the forks of branches (Yamashina 1934; Nakane 1989; Morioka and Sakane 1978; Higuchi et al. 1993; Ueda et al. 1993), however, in 1995 we found the first example of a nest built in a tree cavity (Fig. 1). The nest was found on May 5, 1995, in a secondary broad-leaved evergreen forest, where it was located in the trunk of a 15m-high *Casuarina equisetifolia*, 7.1 m above the ground. The tree cavity entrance was 20 cm high and 5 cm wide. The nest, a deep cup made of the leaf fibers of *Pandanus boninensis*, was the same shape as those built on the forks of branches.

One juvenile was seen to leave the nest on May 13, 1995, however the male parent (identifiable by its color-rings) was observed carrying nesting material into the cavity again on June 4. The left tarsus of the female parent was mutilated on June 22 and the pair stopped breeding. A few weeks later the female disappeared from the territory. Although the male remained in the territory, it did not use the tree cavity for nesting in 1996.

Species that do not usually nest in tree cavities on the mainland, sometimes use such cavities on islands; similarly, species may use cavities on islands while their close relatives on the mainland do not use them. For example, Ijima's Leaf-Warbler *Phylloscopus iijimae*, and the Izu Islands Thrush *Turdus celaenops* have both used cavities for nesting on the Izu Islands (Higuchi, H. unpublished data), whereas their closest

relatives *Phylloscopus* leaf-warblers and *Turdus* thrushes of the Japanese mainland do not (Kiyosu 1978). Similarly, the Izu Islands' subspecies of the Japanese Robin *Erithacus akahige tanensis* and the Ryukyu Robin *E. komadori* of the Japanese southwest islands have also used cavities for nesting in (Kiyosu 1978; Higuchi, H. unpublished data), whereas their closest relative *E. a. akahige* of the Japanese main islands has not (Kiyosu 1978).



Fig. 1. The nest in a tree cavity.

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It is perhaps the reduction or absence of nest-site competitors that allows insular species or subspecies to use tree cavities for nesting in. As with the other insular forms already mentioned, the honeyeater may be able to use tree cavities simply because of the absence of nest competitors. Birds that typically nest in tree cavities are absent from the Bonin Islands, whereas on the Japanese main islands there are many cavity nesters ranging in size from owls and woodpeckers to sparrows and tits. In many habitats nest cavities are a limited resource and cavity nesting species are known to compete for available cavities (e.g. van Balen et al. 1982; Carlson et al. 1998). It is possible that this case of cavity nesting by the honeyeater, and the other examples of cavity nesting among island species mentioned above, are examples of ecological release on islands (e.g. Baker-Gabb 1986).

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SHORT COMMUNICATION

Seasonal variation of plumage color in Japanese Light-vented Bulbul *Pycnonotus sinensis orii* in the Yaeyama Group, Southern Ryukyus

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The Light-vented Bulbul *Pycnonotus sinensis* is widely distributed in East Asia. This species is divided into five subspecies (Rand & Deignan 1960). Among them, the Japanese subspecies, *P. s. orii*, was first described from Yonagunijima, the Yaeyama Group by Kuroda (1923) (Fig. 1). This subspecies was characterized by having a narrow white nape patch and a dark brown chest band (Fig. 2A, B). Later, Kuroda (1930) found another color morph with a wide white nape patch and a faint brown chest band on Ishigakijima, also in the Yaeyama Group. This he described as a new subspecies, *P. s. kobayashii* (Fig. 2C, D), however, in 1936 the same color morph was also collected from Yonagunijima (Fig. 2E, F), and subsequently the Ornithological Society of Japan (1942) regarded *P. s. kobayashii* as a junior synonym of *P. s. orii*.

Nakamura and Hanawa (1987) investigated museum specimens of *P. s. orii*, and considered that the appearance of “kobayashii” color morph might result from invasion of the Taiwanese *P. s. formosae*, which has a wide white nape patch, into the Yaeyama Group and subsequent hybridization with Japanese *P. s. orii*. It has been shown, however, that the width of the white nape patch changes seasonally in the continental subspecies *P. s. sinensis* and *P. s. hoyi*. According to Traylor (1967), and Mauersberger and Fischer (1992), the white nape patch becomes wider as a result of a partial pre-nuptial molt in spring, and becomes narrower as a result of a complete post-nuptial molt in late summer. The same might also be true of the Japanese subspecies *P. s. orii*.

The type specimens of *P. s. orii* and *P. s. kobayashii* were collected during different seasons; that of *P. s. orii* in September and that of *P. s.*

kobayashii in April. It seems plausible therefore that the two color morphs may in fact correspond to winter and summer plumage as observed in the continental subspecies. In order to investigate possible seasonal change in plumage color, I examined the plumage variation of specimens of *P. s. orii* in museum collections.

MATERIALS AND METHODS

A total of 26 adult specimens of *P. s. orii* were examined. The specimens were collected from Yonagunijima, Iriomotejima, Haterumajima, Kuroshima, and Ishigakijima in the Yaeyama Group (Fig. 1). A population established on Okinawajima in the mid 1970s was tentatively identified as *P. s. orii* by the Ornithological Society of Japan (2000), but its taxonomic status has not been confirmed yet. Therefore, I did not include Okinawajima sample in the present analyses.

The following specimens were used for the present study: 17 specimens from Yonagunijima (Kanagawa Prefectural Museum of Natural History (KMNH) 11–16; Kyoto University Museum (KUZ) 18, 25; Yamashina Institute for Ornithology (YIO) 24181, 24193, 24194, 24203, 24214, 24217, 24219, 24224, 24225); three specimens from Iriomotejima (National Science Museum (NSMT) 9046, 9058; YIO 88.0343); two specimens from Haterumajima (Okinawa Prefectural Museum (OPM) uncatalogued); three specimens from Kuroshima (NSMT A15067–A15069); and one specimen from Ishigakijima (YIO 12740).

For each specimen, two characters were examined: the width of the nape patch (NP), and the darkness of the chest band (CB). The width of the NP was classified into five categories (I–V), along a continuum from narrow (I) to wide (V). The color of the chest

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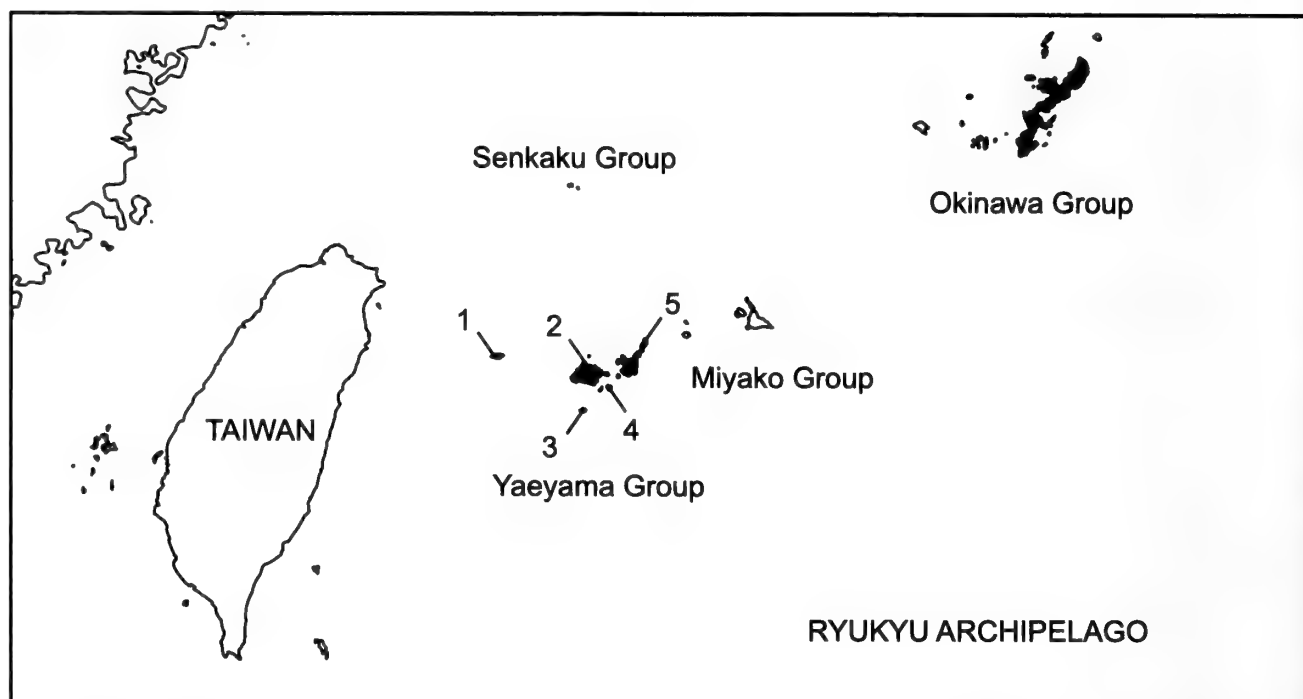


Fig. 1. The distribution of *Pycnonotus sinensis orii* (shaded islands). Localities of specimens used in the present study are: 1 Yonagunijima, 2 Iriomotejima, 3 Haterumajima, 4 Kuroshima, and 5 Ishigakijima.

band was classified as ranging from dark (I) to faint (III). Preliminary analysis of the largest sample, from Yonagunijima, revealed no significant sex-related variation in these two characters ($P > 0.05$: Mann-Whitney's U-test). Therefore, data for males and females were pooled for the analyses.

RESULTS

The width of the nape patch and the coloration of the chest band varied from II to V and from I to III, respectively. Out of the 26 specimens, five exhibited characteristics reported in the original description of *P. s. orii* (a narrow NP (I–III) in combination with a dark CB (I)), while eleven showed characteristics given in the original description of *P. s. kobayashii* (a wide NP (IV–V) in combination with a faint CB (II–III)). The remaining ten specimens had a narrow NP combined with a faint CB. I have named these three color morphs as *orii*-type, *kobayashii*-type and intermediate-type. No specimens were found to have a wide NP in combination with a dark CB. All three color morphs occurred in the western part (Yonagunijima) and in the eastern part (Iriomotejima, Haterumajima, Kuroshima, and Ishigakijima) of the Yaeyama Group. The proportions of the three color morphs did not vary significantly between these two

areas of the Yaeyama Group ($P > 0.05$: Fisher's exact test).

There was, however, seasonal variation in the numbers of the three color morphs (see Table 1). The *orii*-type was found only from September through December, while the *kobayashii*-type was found only from April through August. The intermediate-type bridged the appearance of the other types, being found only from December through June. The nape patch of the specimens collected from September through March was significantly narrower than that of specimens collected from April through August ($P < 0.01$: Mann-Whitney's U-test). The chest band became significantly fainter from September through August ($P < 0.001$: Kendall's rank correlation test).

DISCUSSIONS

The present results strongly indicate that *P. s. orii* undergoes a seasonal plumage change, just as the continental subspecies *P. s. sinensis* and *P. s. hoyi* do. It seems that two color morphs, the *orii*-type and the *kobayashii*-type, which were originally described as different subspecies by Kuroda (1923, 1930), actually correspond to winter and summer plumages.

This seasonal change in plumage color may result from molting in spring and autumn and from feather

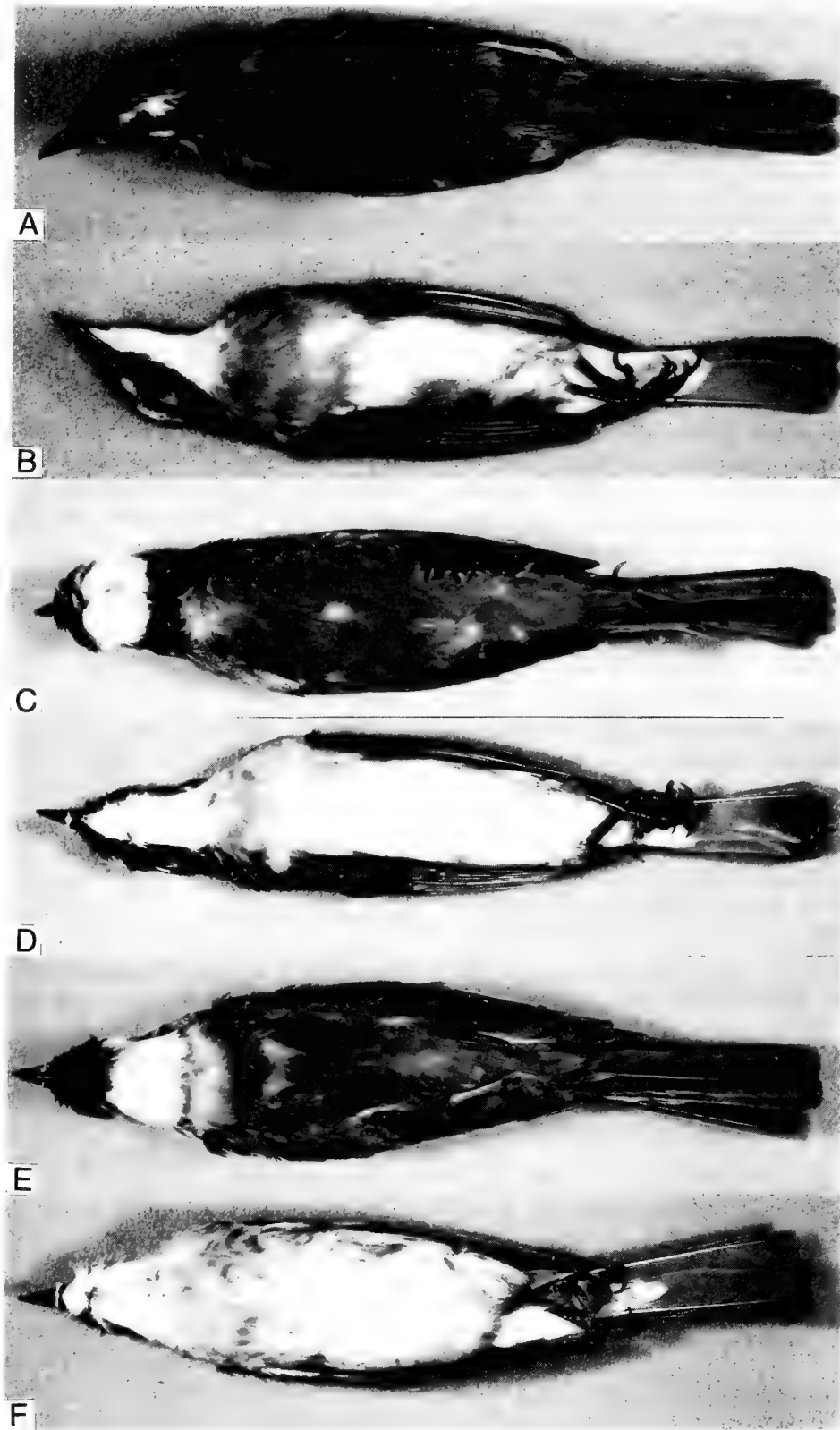


Fig. 2. Dorsal (A,C,E) and ventral (B, D, F) views of *Pycnonotus sinensis orii*. A, B: *orii*-type from Yonagunijima (KMNH 16). C,D: *kobayashii*-type from Ishigakijima (YIO 12740, holotype of *P. s. kobayashii*). E,F: *kobayashii*-type from Yonagunijima (YIO 24194).

Table 1. Seasonal changes in NP width, CB intensity, and the number of color morphs in *Pycnonotus sinensis orii*.

Month	N	NP				CB			Color morph		
		II	III	IV	V	I	II	III	<i>orii</i> -type	intermediate-type	<i>kobayashii</i> -type
September	3	1	2	0	0	3	0	0	3	0	0
December	6	0	6	0	0	2	4	0	2	4	0
March	2	1	1	0	0	0	2	0	0	2	0
April	4	0	2	2	0	0	4	0	0	2	2
June	9	1	1	5	2	0	1	8	0	2	7
August	2	0	0	1	1	0	0	2	0	0	2

wear. The color change patterns identified in the present study suggest that *P. s. orii* molts its nape feathers in spring and autumn, and its chest feathers only in autumn. The chest feathers may gradually become worn over the period from autumn to the next summer. Future direct observations of molt and feather wear will, it is hoped, confirm the present conclusion.

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SHORT COMMUNICATION

Foraging areas of Short-tailed Shearwaters during their northward migration along the Pacific coast of northern Japan

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I studied the distribution of Short-tailed Shearwaters *Puffinus tenuirostris* off the Sanriku and Joban districts of northeastern Japan in April 1999 during their northward migration. Short-tailed Shearwaters breed in southeastern Australia and Tasmania and migrate to the North Pacific in the non-breeding season. During migration, part of the population passes along the coast of northern Japan between April and June (Serventy 1953; Shuntov 1974; Degawa & Watabe 1983; Watabe et al. 1987). In this area, *Euphausia pacifica* is an abundant zooplankton species and is considered to be a key species in food web among marine organisms (Taki et al. 1996; Taki 1998). The distribution pattern and foraging ecology of the Short-tailed Shearwaters during their nomadic phase have been studied in the Bering Sea, where millions of these birds feed predominantly on euphausiids (Ogi et al. 1980; Schneider et al. 1986; Hunt et al. 1996), however, little is known about their ecology during the northward migration period. In the present paper, I discuss the foraging distribution of Short-tailed Shearwaters during this northward migration by analyzing the density and behavior of shearwaters in relation to prey availability.

METHODS

Observations were made from the wing deck (height: 7 m) of the 692 ton R/V *Wakataka-Maru* (Tohoku National Fisheries Research Institute:), from 13 to 23 April 1999 during daylight hours while the ship was underway at a speed of 12 knots (about 22 km/h). I identified, counted, and recorded the behavior of all seabirds seen within an area with a radius of 1,000 m from directly ahead of the ship to 90° off the side of

the ship with the best visibility using 8×56 mm and 20×60 mm image-stabilizer binoculars. Bird behavior was classified as either flying or sitting/foraging. The flight directions of flying birds were recorded as well as the time of each bird sighting. Ship speed and sea-surface temperature (SST) data were recorded at one minute intervals. The ship's position was recorded every 10 minutes. Abundance data were standardized to number of birds/km² every 10 minutes. The method used for observing the birds was the same as that described by Tasker et al. (1984).

Based on oceanographic data collected by the R/V *Wakataka-Maru* and the Japan Fishery Information Service Centre (JFISC) SST isothermal map (JFISC 1999; 15–18 April), the sampling area was divided into the following water masses: the Oyashio Area (OA), characterized by SST <10°C; Transition Area (TA), characterized by SST >11°C; a thermal front (TF) near the 10–11°C SST isothermal line, and a Warm-Core Ring (WCR), which formed from the Kuroshio Extension was characterized by a SST of 11°C, and the WCR remained at 39–40°N, 142–145°E (Fig. 1a).

RESULTS AND DISCUSSION

The total standardized number of all birds recorded during the 3,860 min of observation was 6,130.2 birds belonging to 32 species. The total standardized number of Short-tailed Shearwaters was 2,164.4, which was 35.4% of the standardized total of all birds observed. Thus, this shearwater was the predominant species in this survey area and period (Table 1). The densities of Short-tailed Shearwaters varied widely throughout the survey area, and were high within 50–100 km of the coast (Average±SD: 5.6±13.8 birds/km²; Maximum: 140.4 birds/km², Fig. 1b). Sitting/foraging shearwaters were found on the TF

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Table 1. Species composition and total number of seabirds recorded during the survey off Sanriku and Joban, northern Japan, in April 1999.

Species name	Total
Order Gaviiformes	
Family Gaviidae	
Pacific Loon <i>Gavia pacifica</i>	7.5
Yellow-billed Loon <i>Gavia adamsii</i>	2.0
Order Procellariiformes	
Family Diomedidae	
Laysan Albatross <i>Diomedea immutabilis</i>	40.1
Black-footed Albatross <i>Diomedea nigripes</i>	17.2
Family Procellariidae	
Northern Fulmar <i>Fulmarus glacialis</i>	26.6
Streaked Shearwater <i>Calonectris leucomelas</i>	786.2
Flesh-footed Shearwater <i>Puffinus carneipes</i>	351.2
Sooty Shearwater <i>Puffinus griseus</i>	347.9
Short-tailed Shearwater <i>Puffinus tenuirostris</i>	2,164.4
Family Hydrobatidae	
Fork-tailed Storm-petrel <i>Oceanodroma furcata</i>	0.5
Leach's Storm-petrel <i>Oceanodroma leucorhoa</i>	14.4
Sooty Storm-petrel <i>Oceanodroma tristrami</i>	667.1
Madeiran Storm-petrel <i>Oceanodroma castro</i>	13.9
Order Pelecaniformes	
Family Phalacrocoracidae	
Temminck's Cormorant <i>Phalacrocorax filamentosus</i>	0.6
Pelagic Cormorant <i>Phalacrocorax urile</i>	4.7
Order Charadriiformes	
Family Phalaropodidae	
Red Phalarope <i>Phalaropus fulicarius</i>	345.0
Family Stercorariidae	
South Polar Skua <i>Catharacta maccormicki</i>	0.3
Pomarine Jaeger <i>Stercorarius pomarinus</i>	11.6
Long-tailed Jaeger <i>Stercorarius longicaudus</i>	33.8
Parasitic Jaeger <i>Stercorarius parasiticus</i>	0.8
Family Laridae	
Herring Gull <i>Larus argentatus</i>	20.0
Slaty-backed Gull <i>Larus schistisagus</i>	65.7
Glaucous Gull <i>Larus hyperboreus</i>	0.5
Black-tailed Gull <i>Larus crassirostris</i>	310.2
Black-legged Kittiwake <i>Larus crassirostris</i>	599.9
Common Tern <i>Sterna hirundo</i>	0.3
Family Alcidae	
Thick-billed Murre <i>Uria lomvia</i>	10.4
Marbled Murrelet <i>Brachyramphus marmoratus</i>	0.7
Ancient Murrelet <i>Synthliboramphus antiquus</i>	222.3
Crested Auklet <i>Aethia cristatella</i>	0.3
Parakeet Auklet <i>Aethia psittacula</i>	0.6
Rhinoceros Auklet <i>Cerorhinca monocerata</i>	53.6
Total	6,120.2

and OA waters. Only a few flying birds and no sitting birds were observed in the WCR (Figs. 1b & 1c). Higher proportions (82%) of birds flew northward were recorded during survey period suggesting that they were on migration to northern sea area as described by Ito and Ogi (1999) (Table 2). However at

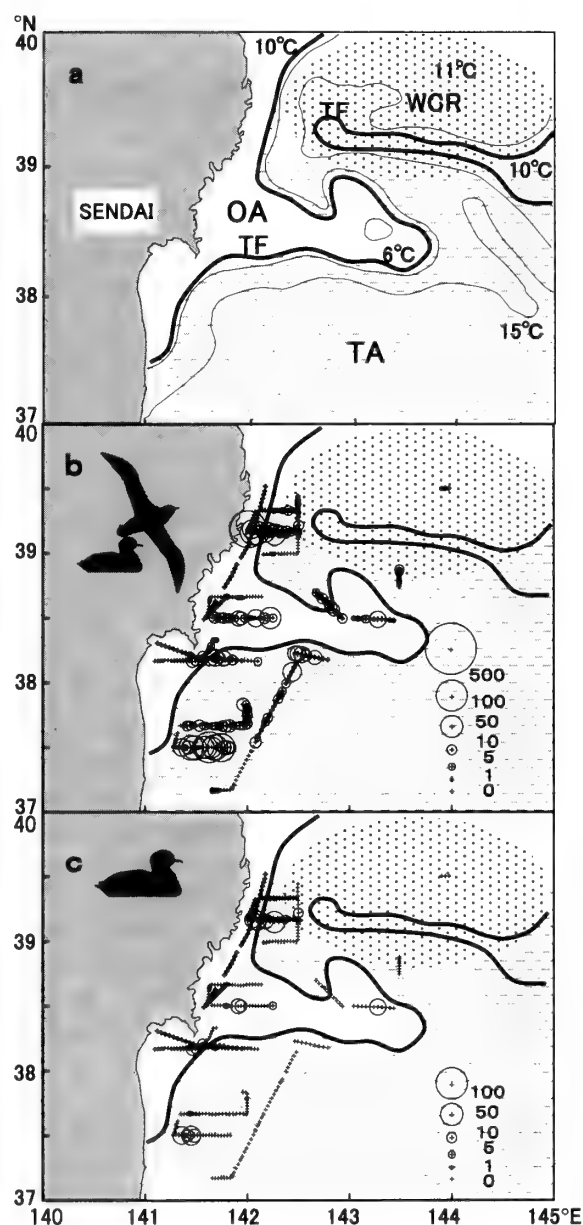


Fig. 1. Oceanographic features during 15–18 April and distribution of Short-tailed Shearwaters off Sanriku and Joban in April. (a) OA: Oyashio Area; TA: Transition Area; TF: thermal front; WCR: Warm-Core Ring; (b) flying and sitting/foraging shearwaters; (c) sitting/foraging shearwaters only. +: position where a 10 minute count was made; the size of the circle represents the abundance of birds at each position (birds/km²).

Table 2. Behavior of Short-tailed Shearwaters recorded for each sighting.

	N	(%)
Flying Northward	1,771.4	81.8
Flying Southward	14.0	0.6
Sitting/Foraging	378.9	17.5
Total	2,164.4	100.0

least five flocks consisting of 100–1,000 Short-tailed Shearwaters (including the birds foraging outside of the sampling radius) were observed on the water at 39°15'N, 142°00'E on 22 April 1999. In these flocks more than 80% of birds were actively diving into the water and they continued foraging until the ship approached closely. Some of them (at least 20 birds) vomited euphausiids before flying away from the ship. Taki et al. (1996), and Taki and Ogishima (1997) reported that *E. pacifica* adults are the most abundant zooplankton in April and they tend to occur in the Oyashio where the water is at 5–10°C (Kotani et al. 1996; Taki et al. 1996; Taki & Ogishima 1997). *E. pacifica* avoids areas of high SST and rarely occurs in the WCR (Taki 1998). In mid April, *E. pacifica* form daytime surface swarms in the coastal area off Sanriku (Endo 1984; Odate 1991) Thus, the distribution of some shearwaters during their northward migration is presumably related to the presence of adult euphausiids in cold water masses off the Sanriku and Joban district.

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SHORT COMMUNICATION

Sexual differences in the external measurements of Black-tailed Gulls breeding on Rishiri Island, Japan

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SCIENCE© The Ornithological Society
of Japan 2002Michiyo CHOCHI^{1,*}, Yasuaki NIIZUMA^{2,#,**} and Masaoki TAKAGI³¹ Department of Ecology and Systematics, Graduate School of Agriculture, Hokkaido University, Sapporo 060–8589, Japan² Institute of Low Temperature Science, Hokkaido University, Sapporo 060–0819, Japan³ Laboratory of Animal Sociology, Faculty of Science, Osaka City University, Sumiyoshi-ku, Osaka, 558–8585, Japan

Sex ratio is an important parameter to consider in ecological and conservation seabirds studies (Weimerskirch & Jouventin 1987). Visually assessing with certainty the sex of live seabirds, however, may be an impossible task when no obvious differences in plumage or body size exist between the two sexes. Several previous studies of Laridae species have shown that males are significantly larger than females (external measurements) and discriminant functions using measurements sex Laridae with great reliability (Shugart 1977; Ryder 1978; Fox et al. 1981; Schnell et al. 1985; Coulson et al. 1983; Evans et al. 1993; Bosch 1996; Rodriguez et al. 1996; Palomares et al. 1997).

The Black-tailed Gull *Larus crassirostris* is a medium-sized gull, endemic to the northwest Pacific, breeding extensively in coastal regions around the Japanese archipelago. Although Black-tailed Gulls are one of the most common seabird species in Japan, little is known about their biology or morphology. Similarly to other Laridae species, Black-tailed Gulls have no sexual differences in their plumage or coloration. This study is aimed at describing the external measurements of Black-tailed Gulls and determining a discriminant function using the measurements to facilitate the sexing of the gulls in the field.

METHODS

A management program controlling the number of Black-tailed Gulls was carried out by the Rishiri

town office on Rishiri Island (45°05'N, 141°07'E), off the northwest coast of Hokkaido, Japan. In this region, gulls are a nuisance to townspeople, inflicting damage on the commercial fishery and affecting flights to and from the airport nearby. Carcasses of gulls culled during the course of this program were used to investigate the relationship between the external measurements and sex.

On Rishiri Island, about 7,900 pairs bred in 1998 and 8,600 pairs in 1999 (Hokkaido Government 1999, 2000), on a 9.12 ha area covered with dwarf bamboo *Sasa nipponica*. Gulls were shot around the colonies from 14–18 June 1998 during the incubation period, and from 17–24 June 1999 during the incubation and hatching periods (Hokkaido 1999, 2000). A total of 237 carcasses was collected and frozen less than one hour after being shot. External measurements were carried out after the carcasses had been thawed.

Ten external measurements were performed following the procedures described in Bosch (1996). Head length (HL), long bill length (LBL), short bill length (SBL), nalis (Nal: the distance from the tip of bill to the nostril), bill depth (BD), tarsus length (Tar), foot length (FL), and middle toe length (MTL) were measured to the nearest 0.01 mm using vernier calipers. Tail length (Tail L: the length between the uropygial gland and the tip of one rectrix) and wing length (WL: natural chord) were measured to the nearest 0.1 mm and 1 mm, respectively, using rulers. Body mass was weighed to the nearest 0.1 g using an electrical balance. Several studies have found sexual dimorphism in body mass for Laridae species (Ingolfsson 1969; Ryder 1978; Threlfall & Jewer 1978; Hunt et al. 1980; Fox et al. 1981; Coulson et al. 1983; Monaghan et al. 1983; Bosch 1996; Rodriguez et al. 1996; Palomares et al. 1997). However, due to its variability throughout the breeding season (Jones

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Table 1. Average values for external measurements and MD index of Black-Tailed Gull. Standard deviations are expressed as \pm SD, and ranges are given in Parentheses. Significance levels were improved using the sequential Bonferroni technique.

Adult	Male (N=139)	Female (N=98)	t-value	P-value	MD index
Head Length (mm)	112.78 \pm 2.66 (105.60–118.99)	103.99 \pm 2.53 (96.82–111.35)	25.55	<0.01	8.11
Long Bill Length (mm)	74.68 \pm 2.84 (62.70–85.20)	69.03 \pm 2.77 (63.10–77.40)	15.24	<0.01	7.86
Short Bill Length (mm)	52.21 \pm 2.12 (46.75–57.10)	47.67 \pm 2.16 (42.40–55.35)	16.11	<0.01	9.09
Nalospa (mm)	24.53 \pm 1.59 (21.44–28.80)	22.39 \pm 1.51 (18.70–28.90)	10.40	<0.01	9.12
Bill Depth (mm)	17.11 \pm 1.24 (14.50–20.67)	15.09 \pm 1.01 (13.30–18.90)	13.32	<0.01	12.55
Tarsus Length (mm)	57.62 \pm 2.15 (49.85–63.35)	53.19 \pm 2.10 (45.60–57.45)	15.76	<0.01	8.00
Foot Length (mm)	104.47 \pm 3.52 (89.45–114.12)	97.36 \pm 3.46 (89.15–111.98)	15.42	<0.01	7.05
Middle Toe Length (mm)	52.12 \pm 2.25 (43.45–57.04)	48.28 \pm 2.34 (39.95–52.01)	12.72	<0.01	7.65
Tail Length (mm)	143.85 \pm 5.83 (126.5–157.0)	136.36 \pm 4.84 (124.3–149.0)	10.43	<0.01	5.35
Wing Length (cm)	39.01 \pm 0.80 (36.5–157.0)	37.39 \pm 0.75 (35.6–39.2)	15.65	<0.01	4.24

1994; Croxall 1995), sexual difference in body mass is not described here (Loretsen & Røv 1994). Once these measurements were collected, birds were dissected and sexed based on their reproductive organs.

Each external measurement was compared between the sexes using Student's *t*-test. Sequential Bonferroni's *t*-test was performed to increase significance power. To compare the degree of sexual difference among measurements, the mean difference (MD) index was used (Agnew & Kerry 1995). The MD index was expressed as the difference of the average measurements between male and female:

$$MD = 200 \times (X.m - X.f) / (X.m + X.f)$$

where *X.m* and *X.f* are the mean of the measurements for males and females, respectively; a larger index indicating greater sexual dimorphism.

Finally, a discriminant function analysis was performed using HL and BD for sex determination of the gull, because these two measurements are readily taken during field studies (Fox et al. 1981; Palomares et al. 1997).

RESULTS

Male gulls were significantly larger than females for all external measurements (Table 1). MD indices

for parameters of the head region, i.e. HL, LBL, SBL, Nal, and BD were larger than those of the extremities, i.e. WL and Tail L. The average body mass of males was 641.2 g \pm 44.0 (SD) and 537.5 g \pm 42.3 for females.

Using HL and BD measurements, the following discriminant function was obtained;

$$D = 150.63 - 1.22 HL - 1.14 BD$$

$$(F_{2,234} = 372.88, P < 0.0001)$$

Both two variables contributed significantly to the function (HL, $F_{1,234} = 324.21$, $P < 0.0001$; BD, $F_{1,234} = 25.41$, $P < 0.0001$). Following this function, birds were classified as males when $D < 0$ and female when $D > 0$. This discriminant function proved reliable for 95.7% of the males (133 out of 139), for 98.0% of the females (96 out of 98), and for a total of 96.6% of the birds (Fig. 1).

DISCUSSION

This study demonstrated that Black-tailed Gulls, breeding on Rishiri Island have marked sexual differences in their external measurements and can be sexed by a discriminant function using HL and BD with a total reliability of 96.6%. This discriminant function will prove useful for sexing Black-tailed

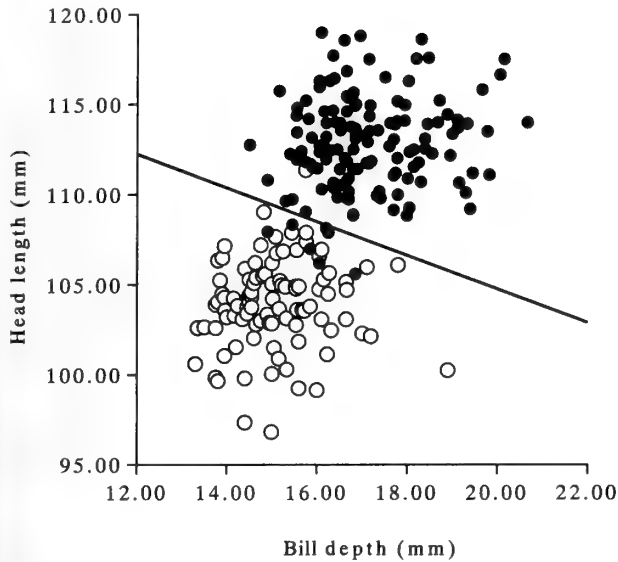


Fig. 1. Relationship between bill depth (BD) and head length (HL) to the function $1.22 \text{ HL} = 150.63 - 1.14 \text{ BD}$. Open circles show females and closed circles show males.

Gulls in the field. Rapid sexing of a bird would contribute to shortening handling time thereby allowing researchers to release birds quickly after a minimum of disturbance. Before applying this method to other populations or age classes, however, sexing accuracy requires further testing, especially since Laridae species show inter-colonial variation in external measurements (Threlfall & Jewer 1978; Monaghan et al. 1983; Jehl 1987; Evans et al. 1993), as well as age related differences (Coulson et al. 1981; Allaine & Lebreton 1990; Palomares et al. 1997). The greater difference in size between the sexes found in the head region indicates that this region, especially the bill, may play an important role, probably in sexual display and territorial defence by males (Ingolfsson 1969). The smaller sexual dimorphism in the wing region may be related to the species' flight performance (Schnell et al. 1985; Croxall 1995).

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SHORT COMMUNICATION

External features and molecular sexing of the anomalous Pintail, *Anas acuta*, found at Hyo-ko Waterfowl Park, Niigata Prefecture, Japan

ORNITHOLOGICAL SCIENCE

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Phenotypic variation of the plumage including albinism and melanism is widely known among birds. On the other hand, morpho-chromatic variation of the plumage caused by hybridization has also been found in nature. Such an example is occasionally found in the Anatidae (Kuroda 1939), and possible hybrids of the Pintail *Anas acuta* with other species, e.g., Mallard (*A. platyrhynchos*), Teal (*A. crecca*), Baikal Teal (*A. formosa*), Gadwall (*A. strepera*), Wigeon (*A. penelope*), Shoveler (*A. clypeata*) and Pochard (*Aythya ferina*), were documented previously (Kuroda 1939). In fact, a presumptive hybrid between the Pintail and Baikal Teal was observed also in Hyo-ko Waterfowl Park, located in a suburb of Niigata City, Niigata Pref., Japan (Chiba, unpubl. data). During the course of bird-banding study in this Park, we incidentally found 2 unusual male Pintails, which were morphologically different from any known hybrids. The present study, therefore, was conducted to clarify the characters of these anomalous Pintails on the basis of macroscopic examination and molecular sexing.

MATERIALS AND METHODS

1) Birds

Thirteen individuals of Pintail were used in this study (Table 1). They were captured (by permission of the Ministries of the Environment and Culture, Japan) at Hyo-ko Waterfowl Park (37°50'N, 139°14'E) in the suburb of Niigata City, Niigata Prefecture, Japan, during 2 winter seasons, from January 2000 to March 2001. The birds were caught humanely by hand-made net or by hand, marked with a metal ring, and kept in plastic cages (80 cm × 50 cm × 25 cm) for a while. Then, their external features were macroscopically examined and recorded in photographs, and measurement of the body was made. Sex and age were checked mainly based on their plumage and cloacal structure. The contour feathers as a source of DNA, 5 to 7 feathers per bird, were plucked from the mid breast region by using sterilized forceps, put into clean plastic bottles, and stored in a refrigerator at –10°C before extracting the DNA. After examination, the birds were released back to the wild.

2) Isolation of genomic DNA

Genomic DNA was isolated from 3 contour feathers plucked from the mid breast of each bird. The method of DNA extraction followed Walsh et al., (1991), Murata & Masuda (1996) and Murata et al. (1998), with a slight modification. Briefly, a length of calamus about 3 mm was removed from the proximal end with clean scissors and cut into smaller pieces, which were incubated in 200 µL of 5%(w/v) Chelex^R (Bio-Rad) at 56°C overnight, and then boiled in a water-bath for 8 min. After centrifugation at 12,000 rpm for 5 min, the supernatant was used as template DNA for PCR.

2) Isolation of genomic DNA

3) PCR for gender determination

Primer sets used in this study for amplifying the Z/W chromosome-specific DNA sequences of Pintail were those used for sexing domestic duck (*A.*

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platyrhynchos var. *domestica*) as reported by Itoh et al. (2001). The sequences of sexing primer for amplifying the W chromosome-specific DNA (~190 bps) were 5'-ACAGTTTGTCTGTCTCCGGGAA-3' (AWS03) and 5'-AGCTGGAYTTCAGWSCATCTTCT-3' (USP3), and those of internal control primer for amplifying the Z/W chromosome-common DNA (~250 bps) were 5'-CTCTGTCTGGAAGGACTT-3' (INT-R) and 5'-ATAGAAACAATGTGGGAC-3' (INT-F). Detailed information about these primers and related sequences was given elsewhere (Itoh et al. 1997, 2001; Ogawa et al. 1997).

PCR was carried out in a 25- μ L mixture containing a 0.2 mM concentration of each dNTP, 50 pmols of primers AWS03, USP3, INT-R and INT-F, 3 μ L of DNA extract, 0.25 units of *Taq* polymerase (Amersham), and 2.5 μ L of 10 \times PCR buffer. The PCR conditions used for the thermal cycler (PE Applied

Biosystems, 9700) were as follow: initial DNA denaturation at 95°C for 3 min followed by 35 cycles of 95°C, 80 sec for denaturation; 59°C, 90 sec for annealing; 72°C, 60 sec for extension, and lastly 72°C, 9 min for final elongation. PCR products (8 μ L) were electrophoresed on a 2% agarose gel (A-6013, SIGMA) in 0.5 \times TBE (44.5 mM Tris-borate, 44.5 mM Boric acid, 0.5 mM EDTA) buffer at 100V for 35 min, stained with ethidium bromide, and visualized under a UV transilluminator.

RESULTS

Externally, 2 birds in question, Sp-1 (ring number, 10A-80409) and Sp-2 (10A-75898), were characterized by nuptial plumage of the male type (Fig. 1A). Measurement values of the wing, tail and body weight of these birds approximately corresponded to



Fig. 1. External features (A) and external aspect of the disclosed vent (B) of an anomalous Pintail (Sp-2). Corresponding part of an adult male with normal plumage (C) and that of an adult female with normal plumage (D) are also shown. dl, dorsal lip of cloaca; p, phallus (artificially everted and erected); vl, ventral lip of cloaca. Scale bar, 1 cm

Table 1. Measurements of anomalous males (SP-1 and SP-2) of the Pintail, *Anas acuta*, and of control (normal plumage) birds for comparison

	Wing*	Tail*	Bill*	Tarsus*	Body Weight**
Sp-1 (10A-80409)	259.0	148.0	46.5	40.8	810.0
Sp-2 (10A-75898)	259.0	173.0	47.3	42.5	790.0
Control					
Normal males (N=5)	260.8±5.4	145.4±38.5	50.6±2.4	41.8±2.0	836.0±50.0
Normal females (N=5)	224.6±10.6	109.8±11.2	47.7±2.0	38.9±2.3	722.0±65.5
"Buff" mutant female	260.0	110.0	45.3	39.0	670.0

*, mm; **, g; Numerals are presented as the average±SD

those of control males rather than to those of control females (Table 1). However, their plumage was unclear in comparison with normal male plumage; i.e., their heads were light brown in color, the breast and upper belly not brilliantly white, but finely striped, the back and sides roughly striped, the black spot on the scapulars indistinct, and the dark undertail coverts and creamy caudal belly unclearly demarcated (Fig. 1A). As so far studied, no morphological evidence of hybridization with other species has been detected in the present birds. Interestingly, neither phallus (Fig. 1C) nor its equivalent in the cloacal region (Fig. 1B), which macroscopically appeared just the same as that seen in the female duck (Fig. 1D).

The W chromosome-specific DNA fragments (~190 bp) were PCR-amplified from feather extracts of 2 unusual males, Sp-1 and Sp-2, one "Buff" mutant female, and normal-plumage females. In contrast, only Z/W chromosome-common DNA fragment (~250 bp) was amplified from normal-plumage males (Fig. 2). No DNA fragment was amplified from negative control (distilled water). Thus, the results indicated that the 2 atypical males in question have DNA sequences common to the sequences of Z and W chromosomes.

DISCUSSION

The present study provided new data available for characterization of unusual individuals of Pintail. The molecular sexing data suggested two possibilities, i.e., (1) that the anomalous birds studied are genetically female (Z/W) irrespective of their male-type plumage and (2) that they represent the individuals of sex chromosomal aberrations, e.g., ZZW. Apart from these possibilities, one may presume that the birds in question are immature (under-yearling) males. However, the third possibility can be excluded, for they

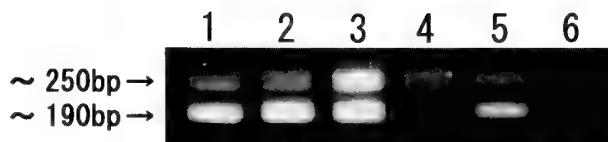


Fig. 2. Electrophoretic pattern of DNA for gender determination of Pintail. The W chromosome-specific DNA fragments (~190 bp) were amplified from plucked contour feathers of anomalous Pintails (lanes 1 and 2), "Buff" mutant female (lane 3) and normal-plumage female (lane 5), while only Z/W chromosome-common DNA fragment (~250 bp) was amplified from normal-plumage male feathers (lane 4). No sex-specific DNA band was observed in the negative control using distilled water (DW, lane 6).

had no phallus in the cloaca, although no anatomical evidence on the gonads was obtained. In favor of this view, a study made long ago showed that immature Mallard males killed between late July and early November had a macroscopically distinct phallus (Höhn 1960). Furthermore, recovery data of the marking showed that at least one of them, Sp-2, was a 2+-year-old adult bird.

If the anomalous birds studied are genetic females, we have to explain why did the genetic females have a male character for their plumage? Previous studies cited in a review paper (Witschi 1961) may be helpful for discussing this point. In the duck, Wolff and Wolff (1949) and Wolff (1950) showed that the development of accessory sex organs, syrinx and phallus, depends on the gonads in the prehatching stages: gonadectomy caused various degrees of masculinization in the female embryos, i.e., the enlargement of syrinx and the development of the phallic tubercle. Unfortunately, however, these studies provided no information about the effect of gonadectomy on the plumage. In birds, it is generally known that gonadectomy or deprivation of sex steroids causes the sex-related characters to turn to the phenotype of the

homozygote (genetic male), not heterozygote (genetic female), of the sex chromosomes. The present birds may be a case of this phenomenon. If so, we may speculate that the present birds may have dysfunctional ovary or they may have been physiologically ovariectomized, presumably in an earlier life stage.

Currently, we have no data to exclude the second possibility, i.e., the sex chromosomal aberration. It is also known that the domestic fowls of ZZW-genotype show masculinization in the post-hatching early life stages (Naito 1998). In any case, we need further information about the anomalous Pintail from studies on the gonads, chromosomes, genes, plasma concentration of sex steroids, and so on. Recent progress made by studies on the Z/W sex chromosomes of birds has been reviewed with respect to the mechanisms of sex determination and sex differentiation (Naito 1998; Ellegren 2001; Mizuno 2001).

So far as we surveyed during the recent 3 years, the incidence of the present anomaly in the study area is estimated to be 0.02–0.03%. Exact causal factor(s) of the anomaly found in the Pintail remain unknown, but it seems to be important to examine possible relationship between the anomaly and the global pollution. Future comprehensive studies on sexually anomalous birds, both in the field and laboratory, may contribute to various aspects of avian biology and environmental chemistry.

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Vol. 1 2002

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CONTENTS OF VOLUME 1

Number 1 January 2002

PREFACE

Higuchi H

From Japan through Asia to the world:
building bridges in ornithological science.

1

EDITORIAL

Ueda K

"Ornithological Science", the new English
publication from Japan.

3

SPECIAL FEATURE

**Interspecific segregation and attraction in
forest birds**

Hino T

Introduction.

5

Loyn RH

Patterns of ecological segregation among forest
and woodland birds in south-eastern Australia. 7

Recher HF, Davis WE Jr & Calver MC

Comparative foraging ecology of five species of
ground-pouncing birds in western Australian
woodlands with comments on species decline. 29

Mönkkönen M & Forsman J

Heterospecific attraction among forest birds:
a review. 41

Seki S & Sato T

The effect of typhoon on the flocking and
foraging behavior of tits. 53

Murakami M

- Foraging mode shifts of four insectivorous birds species under temporally varying resource distribution in a Japanese deciduous forest. 63

Mizutani M & Hijii N

- The effects of arthropod abundance and size on the nestling diet of two *Parus species*. 71

Hino T, Unno A & Nakano S

- Prey distribution and foraging preference for tits. 83

Sodhi NS

- The effects of food-supply on Southeast Asian forest birds. 89

ORIGINAL ARTICLES**Yamagishi S, Asai S, Eguchi K & Wada M**

- Spotted-throat individuals of the Rufous Vanga *Schetba rufa* are yearling males and presumably sterile. 95

Amano HE & Eguchi K

- Nest-site selection of the Red-billed Leiothrix and Japanese Bush Warbler in Japan. 101

Number 2 September 2002**ORIGINAL ARTICLES****Hino T**

- Breeding bird community and mixed-species flocking in a deciduous broad-leaved forest in western Madagascar. 111

Kotaka N & Matsuoka S

- Secondary users of Great Spotted Woodpecker (*Dendrocops major*) nest cavities in urban and suburban forests in Sapporo City, northern Japan. 117

Amano HE & Eguchi K

- Foraging niches of introduced Red-billed Leiothrix and native species in Japan. 123

Unno A

- Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources. 133

SHORT COMMUNICATIONS**Kawakami K & Higuchi H**

- Bird predation by domestic cats on Hahajima Island, Bonin Islands, Japan. 143

Tojo H, Nakamura S & Higuchi H

- Gape patches in Oriental Cuckoo *Cuculus saturatus* nestlings. 145

Brazil M

- Common Raven *Corvus corax* at play; records from Japan. 150

Kawakami K & Higuchi H

- The first record of cavity nesting in the Ogasawara Islands Honeyeater *Apalopteron familiare* on Hahajima, Bonin Islands, Japan. 153

Yamasaki T

- Seasonal variation of plumage color in Japanese Light-vented Bulbul *Pycnonotus sinensis orii* in the Yaeyama Group, Southern Ryukyus. 155

Ito S

- Foraging areas of Short-tailed Shearwaters during their northward migration along the Pacific coast of northern Japan. 159

Chochi M, Niizuma Y & Takagi M

- Sexual differences in the external measurements of Black-tailed Gulls breeding on Rishiri Island, Japan. 163

Chiba A, Murata K, Mizuno S, Honma R & Sugimori F

- External features and molecular sexing of the anomalous Pintail, *Anas acuta*, found at Hyoko Waterfowl Park, Niigata Prefecture, Japan. 167

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ORNITHOLOGICAL SCIENCE

Volume 1 Number 2 September 2002

Contents

ORIGINAL ARTICLES

Hino T

- Breeding bird community and mixed-species flocking in a deciduous broad-leaved forest in western Madagascar. 111

Kotaka N & Matsuoka S

- Secondary users of Great Spotted Woodpecker (*Dendrocops major*) nest cavities in urban and suburban forests in Sapporo City, northern Japan. 117

Amano HE & Eguchi K

- Foraging niches of introduced Red-billed Leiothrix and native species in Japan. 123

Unno A

- Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources. 133

SHORT COMMUNICATIONS

Kawakami K & Higuchi H

- Bird predation by domestic cats on Hahajima Island, Bonin Islands, Japan. 143

Tojo H, Nakamura S & Higuchi H

- Gape patches in Oriental Cuckoo *Cuculus saturatus* nestlings. 145

Brazil M

- Common Raven *Corvus corax* at play; records from Japan. 150

Kawakami K & Higuchi H

- The first record of cavity nesting in the Ogasawara Islands Honeyeater *Apalopteron familiare* on Hahajima, Bonin Islands, Japan. 153

Yamasaki T

- Seasonal variation of plumage color in Japanese Light-vented Bulbul *Pycnonotus sinensis orii* in the Yaeyama Group, Southern Ryukyus. 155

Ito S

- Foraging areas of Short-tailed Shearwaters during their northward migration along the Pacific coast of northern Japan. 159

Chochi M, Niizuma Y & Takagi M

- Sexual differences in the external measurements of Black-tailed Gulls breeding on Rishiri Island, Japan. 163

Chiba A, Murata K, Mizuno S, Honma R & Sugimori F

- External features and molecular sexing of the anomalous Pintail, *Anas acuta*, found at Hyoko Waterfowl Park, Niigata Prefecture, Japan. 167

3804

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23 JUL 2003

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**Vol. 2 No. 1
February 2003**

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SPECIAL FEATURE

Ecology of seed dispersal

INTRODUCTION

Seed dispersal is a process in which immobile plants expand the species range in a wide scale of the distribution. Plants bear fruits with high nutrient value as a reward to animals which transport them. Animals disperse the seeds far from their parent plants. It is an important process to avoid inbreeding around parent plant and includes escaping high mortality of seedling around the parent plant via intraspecific competition with their kin. As a result, most of the fruits have been adapted to dispersal by birds and other animals.

The relationship between the fruiting phenology of fruited plants and frugivorous birds has been investigated in northern temperate region. However, those were mainly restricted to Europe and North America; therefore, we have not so much information on the bird-plant relationship in eastern paleoarctic region. Recently, some plant ecologists and ornithologists are bearing their interests to this subject in Japan. So, we would like to introduce recent advances in studies of seed dispersal in this feature. We have five articles on the seed dispersal in this issue. These are contributed by 13 Japanese plant ecologists and ornithologists and one Madagascar ornithologist. These five articles include essential and important information on seed dispersal in eastern paleoarctic and tropic Madagascar.

Kominami et al. showed the relationships between plant types and frugivorous birds in a primary lucidophyllous forest in southern Japan. They classified 111 tree species into 17 categories according to their phenological traits. Out of fifteen species of birds recorded in the area, eight are main agents for seed dispersal. A group of summer fruit species provided continuous and familiar food for many bird species and maintains a stability of food resources for birds in the evergreen forest.

In their paper Takanose and Kamitani showed a seasonal correspondence between the fruiting phenology of freshly-fruited plants and the abundance of frugivorous birds in deciduous forests in central Japan. In this area, the majority of fruits ripened in the fall when migrating frugivorous birds were most abundant. The Brown-eared Bulbul *Hypsipetes amaurotis* was an important seed disperser, because of its high frequency of occurrence throughout the fruiting season, and its large gape size which allowed it to swallow all sizes of fruits found at the area. As suggested by these two studies made in central and southern Japan, habitat differences is important factor to explain different syndrome in bird-plant relationship.

Food hoarding is another important process of seed dispersal. In his paper, Hayashida is discussing the seed dispersal of a pine species by the nutcracker. Seed caching is essential process of this syndrome. Nutcrackers store seeds of the Japanese stone pine. All mature cones disappeared by mid-October. Almost all the cones were carried away by nutcrackers. The nutcracker is the most important agent for the seed dispersal of the Japanese stone pine. Hayashida found that pine seedlings were growing in clusters. It means that most seedlings originated from nutcracker caches. It is most likely to give rise to some strong bird-plant reciprocal dependence. It is a good example of co-evolution syndrome between birds and plants.

The interaction between fruits and seed dispersers affect diversity of fruit characteristics mediated by the length of retention time in bird's gut. In her paper, Fukui investigated a seed retention time of 16 fruit species in guts of the Brown-eared Bulbul. She measured some fruit characteristics: fruit size, seed size and water content. The bulbuls defecated large seeds more rapidly than small ones. It suggests that the bulbuls have a mechanism to eliminate bulky seeds from their guts rapidly in order to overcome the gut limitation. Large seeds have an advantage of dispersal quantity and small ones have that of dispersal distance contrary to our expectation.

Rakotomanana and other Japanese researchers studied the role of the Velvet Asity *Philepitta castanea* in Madagascar rain forest. Ecology of seed dispersal in this region and the role of this endemic bird species have been left unknown. They found that the seeds transported by the Velvet Asity were less adapted to bird dispersal. It suggests the presence of dispersal agents other than birds in this area. Community structure of the en-

demic fauna and flora of Madagascar must be intensively studied.

We could invite many plant ecologists outside our society as authors when we planned to publish this issue. It was the first step for collaboration between ornithologists and a plant ecologists in Japan. I hope that these papers facilitate ornithologists and plant ecologists who have interest in seed dispersal syndrome in eastern Palearctic region.

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Classification of bird-dispersed plants by fruiting phenology, fruit size, and growth form in a primary lucidophyllous forest: an analysis, with implications for the conservation of fruit-bird interactions

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Abstract To understand the patterns of fruit-bird interactions and to identify species with significant roles that are irreplaceable in these interactions (key species), we classified plant types according to traits relating to frugivory by birds, and analyzed the relationships between plant types and frugivorous birds in a primary lucidophyllous forest in Japan. At the 4-ha study site, 111 plant species were bird-dispersed and 15 common bird species were frugivorous. The growth form of plant species was divided into overstory, understory, and liana. The phenological pattern of fruiting was divided into “summer”, “fall”, and “persistent” from the temporal pattern of the seed rain. Fruits were classified in terms of size, as small, a size widely eaten by birds, and large, a size that is difficult for small birds to eat. Seventeen types of plant were identified in the study site, which were classified according to growth form, phenological pattern, and fruit size. Of these fruits, 14 species were considered to be major species, that is species that are both abundant and important for certain birds, and a further 20 species were identified as complementary species, that is species that compensate for a low diversity or for a temporal lack of the major species. Of the birds, eight species were considered major dispersal agents. The patterns of relationship between fruits and birds overlapped in various ways. No strong relationship in which species of fruits and birds are dependent almost entirely on each other were found. An important species set composed of three key species (*Eurya japonica*, *Cleyera japonica*, and *Cornus controversa*) and a group of summer fruits provided continuous and familiar food for many bird species. The patterns of relationship suggest that conservation of the overall composition of fruit types improves the stability of food resources for birds and facilitates dispersal success for the plants themselves.

Key words Birds, Forest conservation, Frugivory, Fruit-bird interaction, Lucidophyllous forest, Seed dispersal

Interactions between fruiting plants and frugivorous birds (fruit-bird interactions) play an important role in both plant regeneration and food availability for animals. Frugivorous birds contribute to the dispersal success of plants and improve their chances of regeneration (e.g., Howe 1986; Willson 1992; Herrera 2002; Terborgh et al. 2002). Fruits are essential foods for frugivorous and omnivorous animals. Fruits

also support a winter population of bird species that is mainly insectivorous in summer (Sorensen 1981; Herrera 1984). Therefore, a sudden fluctuation in the interaction between fruiting plants and frugivores has a critical effect both on plant and animal populations (Howe 1977; Hawthorne & Parren 2000; Loiselle & Blake 2002; McConkey & Drake 2002).

Fruit-bird interactions are crucial for the conservation of warm-temperate evergreen broad-leaved forest (lucidophyllous forest), which is the most common forest vegetation in southwest Japan. Over 60%

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of woody plant species in lucidophyllous forests produce fruits that are eaten and dispersed by birds (Nakanishi 1994; Kominami et al. 1995), indicating that the regeneration of many plant species depends on frugivory of birds. In recent years, much of the primary lucidophyllous forest in Japan has been lost and most of the remnant forests are small isolated stands (Sato 1983; Hattori & Asami 1998). Some studies in tropical forests have reported that human disturbance causes the impoverishment of frugivores and the disruption of adequate seed dispersal (Kannan & James 1999; McConkey & Drake 2002). Similar concerns must be raised in relation to Japan's forests. To conserve lucidophyllous forests, it is necessary to determine the effects of disturbance on the dispersal success of plants and on food availability for birds.

Understanding the relationship patterns between fruits and birds, and identifying irreplaceable species that play vital roles in fruit-bird interactions (key species) may help to assess the sensitivity of this interaction to habitat disturbance in lucidophyllous forest. Many obvious relationships between fruiting plants and frugivores have been studied, mainly in tropical forests. For example, only large frugivores can successfully disperse large seeds (Wheelwright 1985; McConkey & Drake 2002; Peres & van Roosmalen 2002). Therefore, interactions between fruit and frugivores in tropical forests are often sensitive to the loss of certain species (Howe 1977; Hawthorne & Parren 2000; Loiselle & Blake 2002; McConkey & Drake 2002; Peres & van Roosmalen 2002). Fruit-bird interactions in temperate forests, however, are more diffuse than in tropical forests (Sorensen 1981; Herrera 1984; Skeate 1987; Malmberg & Willson 1988; Debussche & Isenmann 1989; Jordano 1993; but see Wheelwright 1988). Consequently, it has been suggested that component species of the interaction are interchangeable (Noma & Yumoto 1997). We therefore attempted to classify fruit types for an overview of fruit-bird interactions, and to identify the key species of fruiting plants in lucidophyllous forest.

Here, we classify fruit types, using three important traits, and distinguish key species in a primary lucidophyllous forest. First, it is well known that fruit size restricts seed dispersers, because many frugivorous birds prefer fruits that are smaller than their gape width (Herrera 1985; Wheelwright 1985; Jordano 1987; Debussche & Isenmann 1989; Hegde et al. 1991; Fukui 1995). Second, the phenological traits of fruiting are important in defining fruit-bird interac-

tions in temperate forests (Thompson & Willson 1979; Stiles 1980; Sorensen 1981; Skeate 1987; Noma & Yumoto 1997). The fruit maturation pattern and the fruiting period of bird-dispersed plants are often adapted to seasonal fluctuations in fruit consumption by birds (Herrera 1985; Noma & Yumoto 1997). Third, the growth forms of plants are also essential in the relationship. Growth forms determine the fruiting layer. Birds often prefer a specific layer within the forest when foraging for fruit (Hoppe 1987; Malmberg & Willson 1988). Thus, these three traits of fruits can be related to consumption by particular groups of birds. Although plant species can be subdivided into a few large groups based on these traits, a classification using all three traits may illustrate more detailed structure of fruit types.

The classification of fruit types makes an overview of fruit-bird interactions possible. We attempted to detect relationship among species of fruits and birds that are almost entirely dependent on each other. The role of component species in such strong relationships is not compensated for by other species (Howe 1977; McConkey & Drake 2002). Then we attempted to identify fruit species associating with a wide variety of birds. Such fruit species play a driving role in the fruit-bird interactions of a community (Skeate 1987; Debussche & Isenmann 1989). We considered both component species in strong relationships and abundant species in overall relationships as key species. The list of key species thus obtained may contribute to an assessment of the impact of species loss on fruit-bird interactions.

STUDY SITE AND METHODS

1) Study site

The study was conducted at the Aya Research Site, a long-term ecological research site in a well-preserved lucidophyllous forest, covering over 300 ha, in Miyazaki Prefecture, southwestern Japan (32°03'N, 131°12'E). The study site has been described in detail by Tanouchi and Yamamoto (1995), Sato et al. (1999), and Nagamatsu et al. (2002). The annual mean temperature is 14.2°C and the warmth index is 111. The annual precipitation is 3,070 mm. The most abundant soil type is a moderately moist brown forest soil. The dominant canopy species are *Distylium racemosum*, *Persea japonica*, *P. thunbergii*, *Quercus acuta*, and *Q. salicina*. The canopy height ranges from 25 to 32 m. The subcanopy layer is dominated by *Actinodaphne longifolia*, *Camellia japonica*, *Cin-*

namomum japonicum, *Cleyera japonica*, *Eurya japonica*, and *Neolitsea aciculata*. A 4-ha permanent plot for long-term ecological research has been established on a north- to northwest-facing slope at elevations from 380 to 520 m within the study site.

2) Endozoochorous plants

Of the 203 species of higher plants found at the study site (Sato et al. 1999), 140 are woody plants, 43 are herbs, and 20 are ferns. We classified the disseminule forms of the plant species according to van der Pijl (1982). Seed dispersal by frugivores (endozoochory) was considered the disseminule form for fruits with a fleshy portion, such as the pericarp, arillus, perianth, or receptacle. Birds also disperse the dry fruits of several species of Euphorbiaceae and Rutaceae, which have a lipid-rich seed coat (Ueda & Fukui 1992). We considered endozoochory to be the disseminule form of 111 plant species in the study site (Appendix 1). The scientific names of plants followed Ohwi and Kitagawa (1983).

3) Growth form

Initially, we classified the growth forms of plant species according to three categories: the overstory (canopy trees, subcanopy trees, and epiphytes), the understory (small-trees, shrubs, and herbs), and the liana (woody climbers and large herbaceous climbers). At the study site, trees over 10 m high and epiphytes bear fruit in the canopy or subcanopy layers, whereas smaller trees, shrubs, and herbs bear fruit in the understory. Liana species were classified as a separate category, because the fruiting layer fluctuated with the host plant.

4) Seed rain

To measure the seed rain at the study site, we used 263 seed traps. A 1.2-ha core plot (100×120 m) that included all types of microtopography was established within the 4-ha plot. We divided the core plot into 120 grids (each 10×10 m), and positioned seed traps at the intersections and centers of every grid. Each trap consisted of a polyester cloth cone supported by a circular fiberglass frame, with an area of 0.58 m², placed 1 m above the ground. Seeds that fell into the traps were collected monthly from May 1991 to October 1995 (54 months). All seeds larger than 1 mm in diameter were identified and counted. The collected seeds were classified as either pulpless seeds or seeds with pulp. We considered seeds with pulp to have fallen because of their weight only, and the

pulpless seeds to have been dispersed by birds. Rain-wash and pulp-consuming insects might also have removed pulp, but as the polyester cloth of the traps allowed good ventilation, the trapped material dried quickly, and neither pulp-consuming insects nor rotten fruit were observed in our traps.

5) Fruit phenology

The phenological patterns of fruiting and dispersal in the study site were divided into the following three types, based on phenological studies of seed dispersal by birds in temperate forests (Thompson & Willson 1979; Stiles 1980; Skeate 1987; Nakanishi 1991; Noma & Yumoto 1997): “summer” fruit begin to ripen from late spring to summer, and the fruit are often removed quickly; “fall” fruit ripen from late summer to fall, and most fruit are removed in the fall; and “persistent” fruit are borne for a long period, from fall to winter. We used the seed rain data for the largest seed crop year to determine the phenological type of 50 species. Seed rain data for a combined period of three or four years were used to determine the type for five species for which the seed rain in any one year was less than 15 seeds. We were unable to distinguish the seeds of *Persea japonica* from *P. thunbergii* in the seed rain. Seed rain data of *Persea* in 1992 were used to determine the phenological type of *P. japonica*, because most *Persea* seeds with pulp were found to have fallen beneath *P. japonica* trees, and pulpless seeds were distributed round *P. japonica* trees in 1992. No suitable data were available for determining the type of *P. thunbergii*. Of 55 species with insufficient seed rain data (<15 seeds in five years in total) at the study site, the types of six species were determined using the phenological patterns of fruiting and dispersal reported in other lucidophyllous forest in southwestern Japan (Noma & Yumoto 1997). In all, the phenological types of 62 species (56% of the endozoochorous species in the flora) were classified.

6) Fruit size

To measure the fruit size of endozoochorous species in the flora of the study site, we used fruit and seed specimens collected in Japan. The shorter diameters of fruits and seeds were measured, because the shorter diameter of an ovoid fruit is more likely to be significant in preventing birds from swallowing the fruit than its longer diameter (Karasawa 1978; Fukui 1995). For Celastraceae and Magnoliaceae fruits, measurements of seeds with an arillus were treated as

“fruit size” while those without the arillus were treated as “seed size”. The size of the receptacle was treated as “fruit size” for *Podocarpus macrophyllus* (Podocarpaceae). The seed coat of *Evodia meliaefolia* (Rutaceae) was thin; therefore, we used the same value for “seed size” (seed size without seed coat) and “fruit size” (seed size with seed coat). We measured the fruit size of 57 species (51% of the endozoochorous species) and the seed size of 99 species (89%). For the other species, we used the diameters reported in Karasawa (1978), Kitamura and Murata (1981), Satake et al. (1982), Takushi (1983), Satake et al. (1989), Nakanishi (1996), Noma and Yumoto (1997), and Nakayama et al. (2000). We used the fruit and seed sizes of 107 species for our analyses.

7) Fruits eaten by birds

We recorded the bird species observed in the core plot during the monthly seed-trap collections from 1991 to 1995. The fruit species eaten by these birds were identified from descriptions of their food habits in the literature (Mizobuchi 1958; Fennell 1965; Ogasawara 1968; Chiba 1969; Nakamura 1970; Chiba et al. 1972; Kiyosu 1978; Nakagoshi 1982; Moriyama et al. 1985; Nimura 1988; Narita et al. 1989; Nakanishi 1991; Fukui 1995; Noma & Yumoto 1997). The sizes of fruits and seeds eaten by birds were measured or determined from the literature. The growth forms of all plants were defined as either overstory, understory, or liana. Plant species from cool temperate forests were included for analysis of the fruit size and growth form preferences for each bird species. The scientific and English names of birds followed The Ornithological Society of Japan (2000).

8) Plant abundance

Tree censuses, systematic sampling by quadrat method, and data from seed traps were used to quantify the abundance of each plant species in the study site. All trees and lianas greater than 5 cm in dbh were identified within the 4-ha plot (4,856 individuals) in 1993. The number of individuals in the 4-ha study plot was used to quantify the abundance of each tree and liana species. We established 441 quadrats (4 m² each) at the every intersections of 10×10-m grid in the 4-ha plot, and recorded shrub and herb species in each quadrat in 1991. The number of quadrats including a focal species was used as an indication of the abundance of the species. Fruit abundance of each species was evaluated from the total number of fruits that fell into 263 traps in 54

months. To convert the numbers of seeds in trap data to numbers of fruits, we counted the numbers of seeds per fruit using specimens of 89 species. For 20 species, we used the seed numbers per fruit reported in Nakayama et al. (2000). The number of *Persea* fruits was combined for *P. japonica* and *P. thunbergii*.

RESULTS

1) Growth forms of fruit species in the Aya Research Site and in the diet of birds

The disseminule form of 108 (80%) of the 140 woody plant species in the Aya Research Site involved endozoochory (Appendix 1). High proportions of shrubs (93%), lianas (84%), and trees (70%) were endozoochorous, while only three (7%) herb species were endozoochorous.

Thirty-seven endozoochorous species fruiting in the overstory included 36 species of canopy and sub-canopy trees and one woody epiphyte species (Appendix 2). There were 53 endozoochorous understory species: 23 small trees, 27 shrubs, and three herbs. There were also 21 endozoochorous liana species.

Thirty-seven bird species were observed in the 1.2-ha plot from 1991 to 1995. We identified 15 common species of frugivorous birds (Table 1). Endozoochorous fruits are included in the food habits of 25 of these bird species. Of the frugivorous birds, eight species (Chinese Bamboo Partridge *Bambusicola thoracica*, Jungle Crow *Corvus macrorhynchos*, Blue-and-white Flycatcher *Cyanoptila cyanomelana*, White-backed Woodpecker *Dendrocopos leucotos*, Oriental Turtle Dove *Streptopelia orientalis*, Brown Thrush *Turdus chrysolaus*, Dusky Thrush *T. naumanni*, White's Thrush *Zoothera dauma*) were rare in the plot. These were observed only once or twice during the five year observation. Long-tailed Tit *Aegithalos caudatus* and Grey Bunting *Emberiza variabilis* were common in the plot, but each is reported to eat only one endozoochorous fruit (*Rhus javanica* and *Eurya japonica*, respectively) (Kiyosu 1978; Nimura 1988). Non-frugivorous birds observed in the plot were Sparrowhawk *Accipiter nisus*, Jungle Nightjar *Caprimulgus indicus*, Horsfield's Hawk Cuckoo *Cuculus fugax*, Little Cuckoo *C. poliocephalus*, Oriental Cuckoo *C. saturatus*, Ruddy Kingfisher *Halcyon coromanda*, Ashy Minivet *Pericrocotus divaricatus*, Fairy Pitta *Pitta brachyura*, Nuthatch *Sitta europaea*, Hodgson's Hawk-eagle *Spizaetus nipalensis*, Black Paradise Flycatcher *Terpsiphone atrocaudata* and Short-tailed Bush Warbler *Urosphena*

Table 1. Common frugivorous birds in the study site, and number of fruit species in the diets of the bird, identified from the literature (see Methods).

Species	Season ^a	Weight ^b (g)	No of fruit species ^c					O/U ^d
			O	U	L	Total	Aya	
Brown-eared Bulbul	R	60–75	50	81	16	147	57	0.6
Copper Pheasant	R	745–1348	11	29	8	48	21	0.4
Pale Thrush	F, W	67–77	11	16	2	29	17	0.7
Japanese Green Woodpecker	R	120–136	8	13	5	26	10	0.6
Jay	R	122–147	7	13	3	23	12	0.5
Japanese White-eye	R	9–11	7	15	1	23	11	0.5
Japanese Green Pigeon	R	217–300	13	8	1	22	11	1.6
Narcissus Flycatcher	S, F	14–17	5	9	2	16	7	0.6
Red-flanked Bushrobin	W	12–17	0	11	2	13	8	0.0
Masked Grosbeak	R	63	6	3	2	11	6	–
Japanese Pygmy Woodpecker	R	12–21	3	4	3	10	4	–
Great Tit	R	14–16	2	3	1	6	2	–
Eye-browed Thrush	F	50–117	4	1	0	5	2	–
Bush Warbler	F, W	14–18	1	3	1	5	1	–
Varied Tit	R	14–20	0	2	1	3	3	–

^a R, resident observed in all seasons; S, observed in spring and summer; F, observed in fall; W, observed in winter.

^b Body weight described in Kiyosu (1978).

^c O, overstory; U, understory; L, liana; Aya, species in flora of the study site.

^d Proportion of number of overstory species to understory calculated for bird species that ate at least ten species of overstory and understory fruits in total.

squameiceps.

Both overstory and understory fruits were eaten by most of the common frugivorous birds (Table 1). The ratio of the number of overstory to understory species in the diet (O/U) was calculated for nine bird species that ate at least ten species of overstory and understory fruits in total. For seven bird species, O/U ranged from 0.4 to 0.7, however, the differences between the bird species were not significant (chi-square test, $P>0.05$). O/U exceeded 1.0 only for the Japanese Green Pigeon *Sphenurus sieboldii* (1.6). It was significantly different from the O/U of Brown-eared Bulbul *Hypsipetes amaurotis* (chi-square test, $\chi^2=4.20$, $P=0.040$), Japanese White-eye *Zosterops japonicus* ($\chi^2=3.90$, $P=0.048$), Copper Pheasant *Syrnaticus soemmerringii* ($\chi^2=6.83$, $P=0.009$), and Red-flanked Bushrobin *Tarsiger cyanurus* (Fisher's exact probability test, $P<0.001$), but not significantly different from the O/U of Narcissus Flycatcher *Ficedula narcissina*, Jay *Garrulus glandarius*, Japanese Green Woodpecker *Picus awokera*, or Pale Thrush *Turdus pallidus* (chi-square test, $P>0.05$). Overstory fruits were not found in the diet of the Red-flanked Bushrobin. The O/U of this species differed significantly from those of the six other bird

species (Fisher's exact probability test, $P<0.05$), except Japanese White-eye ($P=0.067$) and Copper Pheasant ($P=0.093$). The fruits of lianas were also eaten by every common bird species except Eye-browed Thrush *Turdus obscurus*.

2) Phenological pattern of fruits and seasonal changes of birds

Depending on the phenological patterns of fruiting and dispersal at the study site, the fruiting species were divided into 10 "summer species", 24 "fall species", and 22 "persistent species", according to the temporal pattern of the seed rain. Seed rain was observed for six species for one to three months from April to June, and for four species mainly from June to August (Fig. 1). These species were considered to be of the "summer" type. Summer fruits were produced during the breeding season of birds, and seed dispersal by birds coincided with fruit ripening. Seed rain for seven species was observed for one to four months from June to October, and for 17 species for two to seven months from June to December (Fig. 2). These species were considered to be of the "fall" type. Fall fruits were presented during the fall migration season of birds, and most of the fruits either were

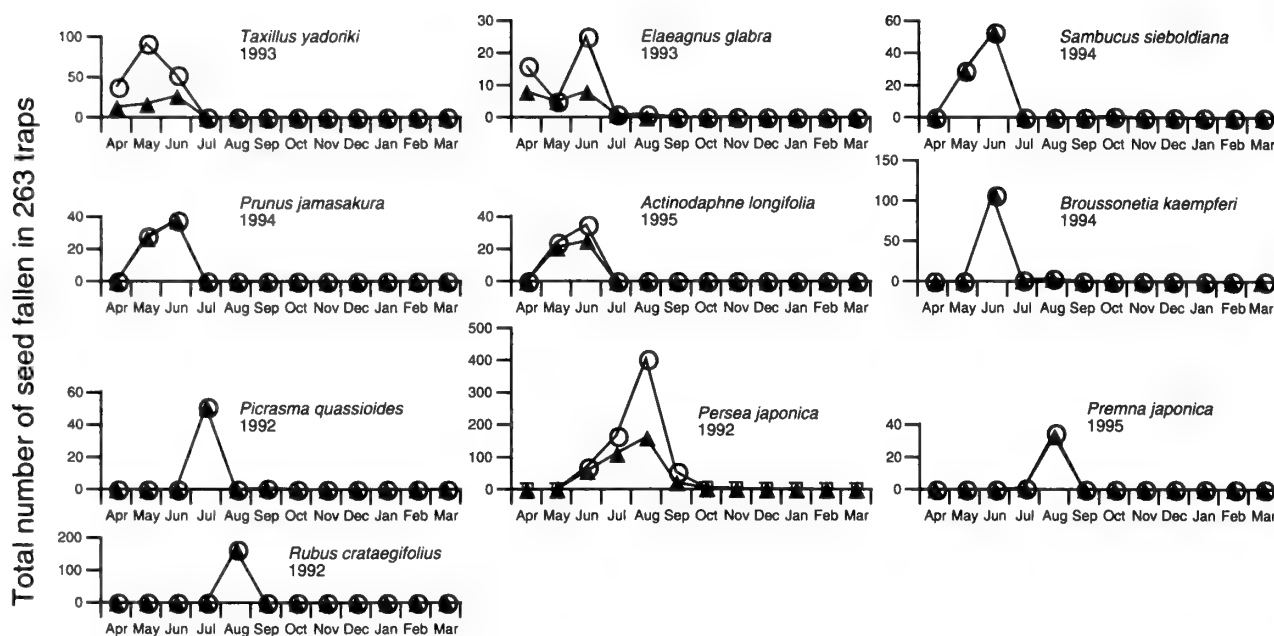


Fig. 1. Seasonal patterns of seed rain for summer species. Solid triangles indicate total numbers of bird-dispersed seeds in 263 traps, and open circles indicate total numbers of all seeds (dispersed by birds + fallen under own weight). The year for the data follows the name of each species.

eaten or fell before January. In the fall type, the bird-dispersed seed rain peaked in early (August and September) or late (October to December, often in November) fall. Seed rain for 22 species was observed for three to eight months, from August until the following April (Fig. 3). These species were considered to be of the "persistent" type. Persistent fruits remained on the tree from fall into winter (and sometimes until the following spring), and the seeds were dispersed by birds mainly during late fall or winter. Of the species for which there were few seed rain data, six were classified as follows: *Myrica rubra* and *Persea thunbergii* (summer type), *Daphniphyllum teijsmannii* and *Syzygium buxifolium* (fall type), and *Myrsine seguinii* and *Vaccinium bracteatum* (persistent type) (Noma & Yumoto 1997).

Ten common frugivorous bird species were observed in the study site in all seasons, while five occurred in specific seasons (Table 1). The Narcissus Flycatcher was a summer visitor that was observed until November. The Eye-browed Thrush was observed only in the late fall migration season (October to December), and the Pale Thrush was observed from late fall through winter (November to March). Although the Bush Warbler *Cettia diphone* was a resident of the forest edge 200 m from the study site, it was observed under the closed forest only from fall to

winter. The Red-flanked Bushrobin was observed only in winter (December to March).

3) Fruit size

Fruits were classified in terms of size as "small" (fruits eaten by birds with a wide range of body sizes), and "large" (fruits that are difficult for small birds to eat). The fruits eaten by seven of the common small frugivorous bird species (i.e., body weight <30 g: Bush Warbler, Japanese Pygmy Woodpecker *Dendrocopos kizuki*, Narcissus Flycatcher, Great Tit *Parus major*, Varied Tit *P. varius*, Red-flanked Bushrobin, and Japanese White-eye) (Table 1) were mainly those with diameters <10 mm (Fig. 4), although one extremely large fruit (fruit diameter 45 mm; but seed 4 mm: *Akebia quinata*) was eaten by three of the small bird species. Seed size was also related to the fruit composition in the food habits of the birds; few of the small birds ate fruits containing seeds that had a shorter diameter exceeding 5 mm. The same tendency for fruit and seed sizes was found in the food habits of both the Japanese Green Woodpecker and the Japanese Green Pigeon (body weight >100 g each). Over 20% of the fruit species eaten by six medium or large bird species, with body weights >50 g (Masked Grosbeak *Eophona personata*, Jay, Brown-eared Bulbul, Copper Pheasant, Pale Thrush,

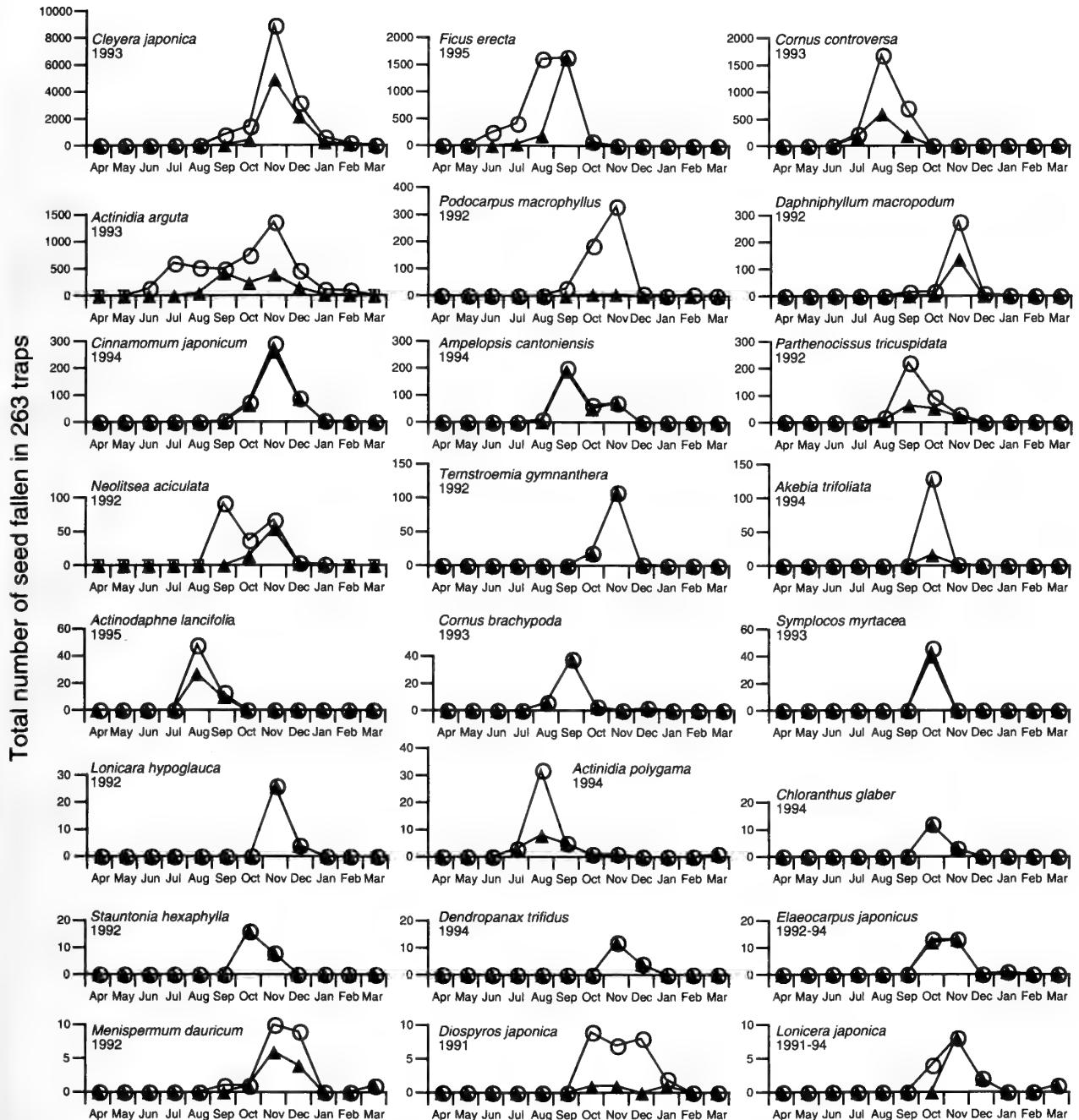


Fig. 2. Seasonal patterns of seed rain for fall species. The symbols are the same as in Fig. 1.

and Eye-browed Thrush), had a fruit size of at least 10 mm or a seed size of at least 5 mm. The diet of the Brown-eared Bulbul included fruits with a wide range of fruit and seed sizes. Therefore, fruits with a fruit size <10 mm, and a seed size <5 mm, were considered as small, and the other fruits were considered as large. Of the 111 endozoochorous species at the study site, the fruits of 67 species (60%) were classi-

fied as "small", those of 40 species (36%) were classified as "large"; and four species were unknown.

4) Classification by all three traits

Endozoochorous species occurring in the study site were classified using the three traits related to avian frugivory (Table 2). Of the eighteen possible types (3 phenological patterns \times 3 growth forms \times 2 sizes),

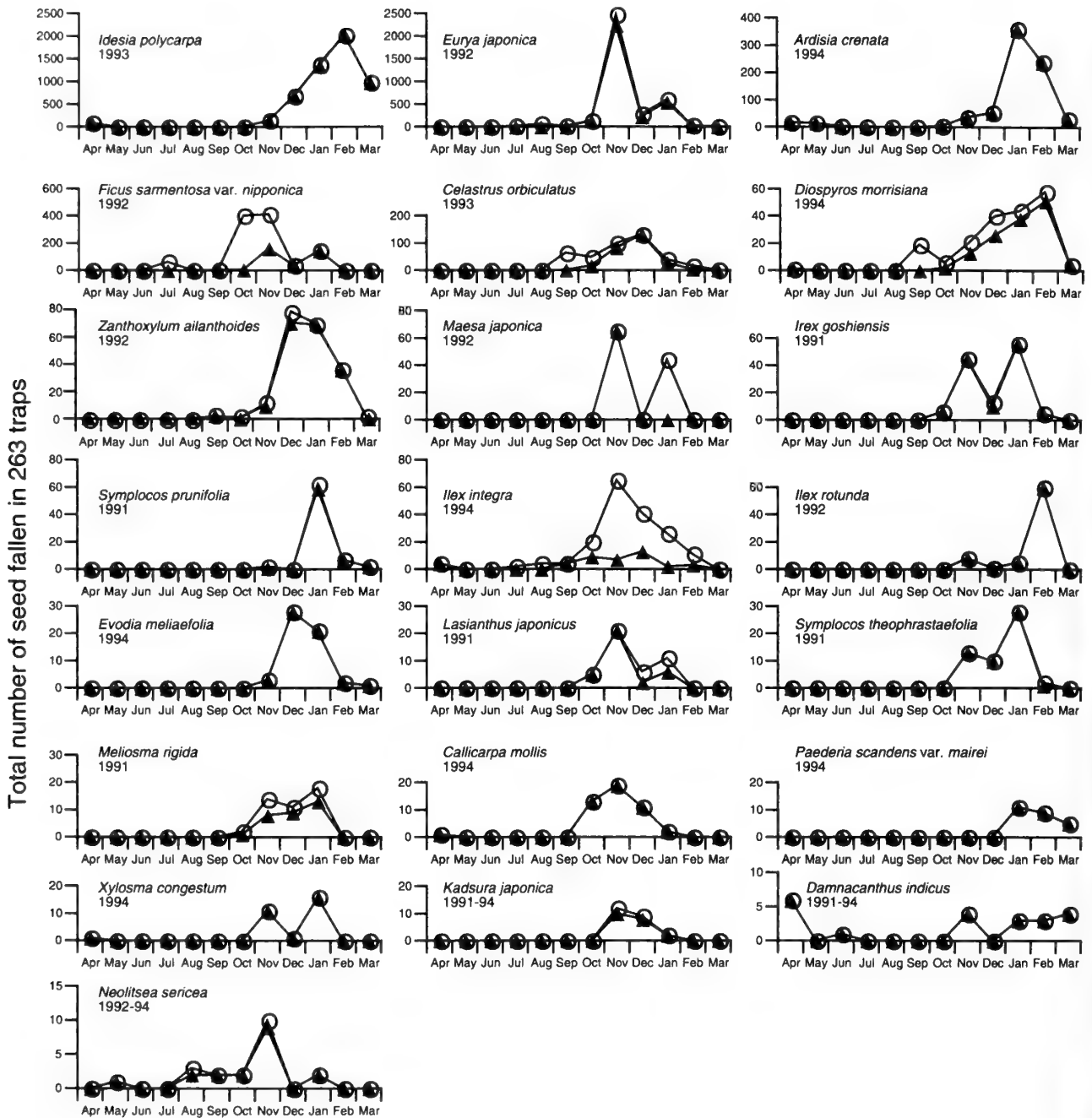


Fig. 3. Seasonal patterns of seed rain for persistent species. The symbols are the same as in Fig. 1.

only one of the expected combinations was not found (summer-liana-large). For the overstory type, large differences in the numbers of species and families were not found among phenological patterns or fruit sizes. For the understory type, 68% of the species and 75% of the families produced small fruits.

Four fruit types (fall-overstory-small (FOS), fall-overstory-large (FOL), summer-overstory-large (SOL), and persistent-understory-small (PUS)) were

relatively abundant in the study site (Fig. 5). In the overstory, the total number of individuals with dbh >5 cm in the 4-ha plot producing FOS, FOL, and SOL fruits was 1104 (51% of all overstory individuals), 328 (15%), and 650 (30%), respectively. In the understory, 140 individual (84%) small trees produced PUS fruits. PUS fruits of shrub and herb were found in the greatest total number of quadrats (451, 90%).

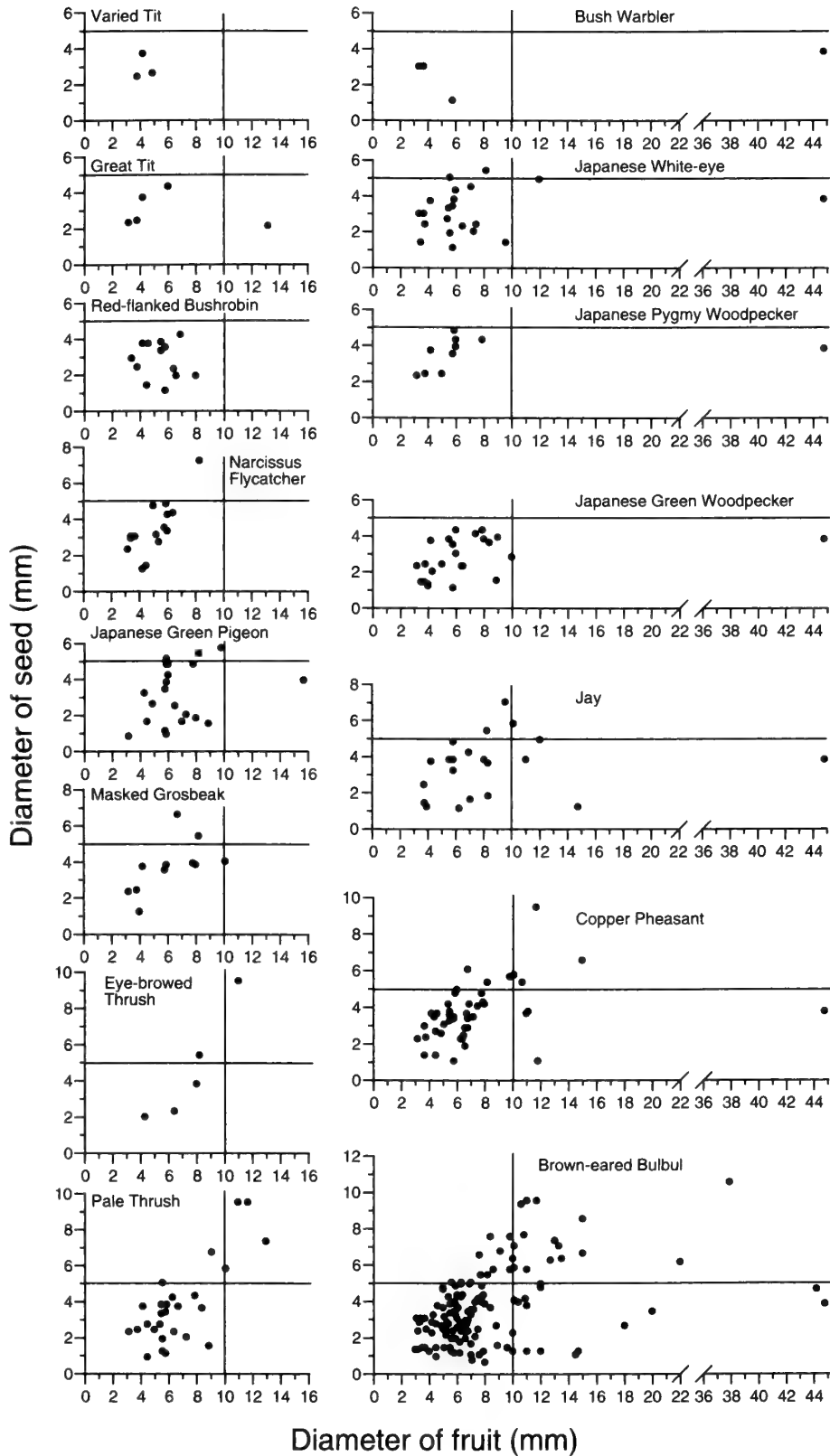


Fig. 4. Size distribution of fruits in the diets of common frugivorous birds. Each dot indicates the fruit and seed size of one plant species. Vertical and horizontal lines indicate the threshold between large and small fruits.

Table 2. Number of species and families (in parentheses) in the classification by three traits (growth form, fruit size, fruiting phenology) related to frugivory by birds.

Growth form	Fruit size	Fruiting phenology				Total
		Summer	Fall	Persistent	Unknown	
Overstory	Large	5 (3)	7 (4)	2 (2)	5 (5)	19 (11)
	Small	2 (2)	4 (2)	6 (5)	6 (4)	18 (12)
	Total	7 (5)	11 (6)	8 (6)	11 (8)	37 (20)
Understory	Large	1 (1)	3 (3)	3 (2)	8 (5)	15 (10)
	Small	2 (2)	3 (3)	10 (8)	21 (17)	36 (21)
	Unknown	0 (0)	0 (0)	0 (0)	2 (2)	2 (2)
	Total	3 (3)	6 (6)	13 (10)	31 (21)	53 (28)
Liana	Large	0 (0)	3 (2)	1 (1)	2 (2)	6 (4)
	Small	1 (1)	5 (3)	2 (2)	5 (5)	13 (9)
	Unknown	1 (1)	1 (1)	0 (0)	0 (0)	2 (2)
	Total	2 (2)	9 (5)	3 (3)	7 (7)	21 (13)
All	Large	6 (3)	13 (9)	6 (5)	15 (12)	40 (22)
	Small	5 (5)	12 (8)	18 (12)	32 (22)	67 (32)
	Unknown	1 (1)	1 (1)	0 (0)	2 (2)	4 (4)
	Total	12 (9)	26 (17)	24 (15)	49 (30)	111 (46)

Twenty-one plant species were common, and nine of the common species were abundant (Fig. 5). In the overstory, 14 species of five types (SOL, FOS, FOL, persistent-overstory-large (POL), and persistent-overstory-small (POS)) were represented by more than 10 individuals each (Fig. 5a). Of these common species, *Cleyera japonica*, *Persea japonica*, *P. thunbergii*, *Cinnamomum japonicum*, *Actinodaphne longifolia*, and *Neolitsea aciculata* were abundant (>100 individuals). *Actinidia arguta*, a fall-liana-large type (FLL), and *Ficus sarmentosa* var. *nipponica*, a persistent-liana-large type (PLL), were common lianas with more than 10 individuals each (Fig. 5b). None of the lianas was abundant. In the understory, *Eurya japonica*, a PUS type, was an abundant small tree with more than 100 individuals (Fig. 5c). None of the other small trees were represented by more than 10 individuals each. Two species of PUS shrubs (*Maesa japonica* and *Damnanthus indicus*) were observed in more than 110 quadrats (>25% of all quadrats, Fig. 5d). *Lasianthus japonicus*, a PUS type, and *Ardisia crenata*, a persistent-understory-large (PUL) type, were also common in the understory, and were observed in 43 quadrats (10%) and 39 (9%), respectively. The other species of shrubs and herbs were observed in fewer than 16 quadrats each (<4%).

Many species provided considerable numbers of fruits (Fig. 5). In the overstory, 11 of 14 common species contributed more than 100 fruits in 54-months seed rain (Fig. 5a). Six overstory species with fewer than 10 individuals each also contributed more than 100 fruits each. Four species of liana contributed more than 100 fruits each, although the populations were of fewer than 10 individuals each (Fig. 5b). In the understory, only three species (*Ardisia crenata*, *Eurya japonica*, and *Ficus erecta*) contributed more than 100 fruits (Fig. 5c, d).

DISCUSSION

1) Major and complementary species of fruits

At the Aya Research Site, plant species provided birds with various fruits of different fruiting phenology, fruit size, and growth form. To understand the pattern of fruit-bird interactions, we defined major and complementary fruit species and distinguished the plant species. A major species was defined as one that produced abundant fruit that was important for a certain bird species. A complementary species was defined as one producing fruit that compensated for low diversity or for a temporal lack of a major species in a particular season.

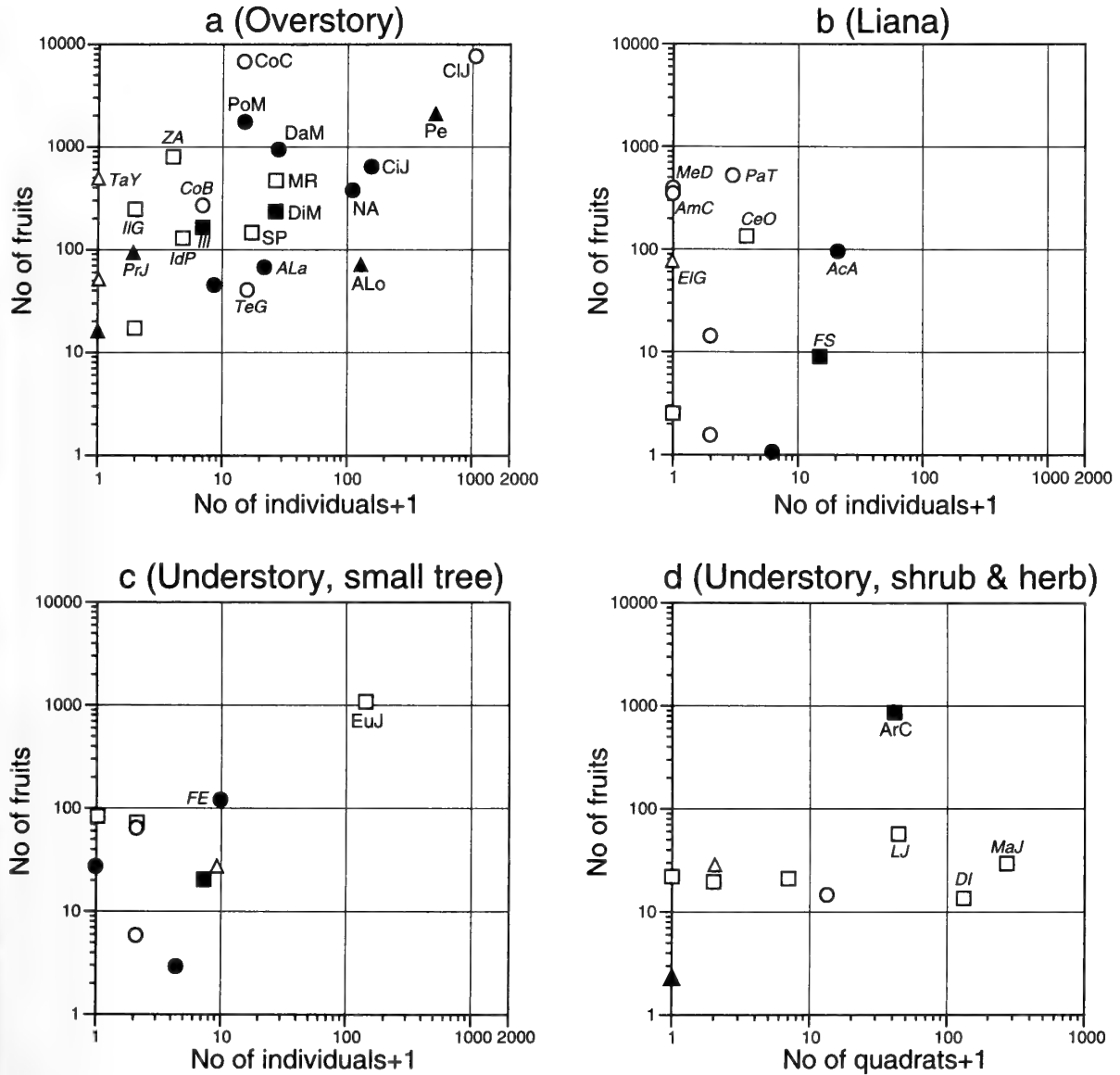


Fig. 5. Abundance of each plant species, classified by traits related to frugivory by birds. The number of individuals with dbh > 5 cm in the 4-ha plot, and the numbers of fruits in 54-months seed rain are shown for each species of overstory (a), liana (b), and small tree (c). The number of quadrats in which each species was observed, out of the 441 quadrats in the 4-ha plot, and the number of fruits are shown for each species of shrub and herb (d). To indicate species that were not counted in the tree census or in the quadrats, one is added to the number of individuals and that of quadrats. Plant types are shown as follows: shape of symbol indicates phenological type (triangle, summer; circle, fall; square, persistent), open symbols indicate small fruits, and solid symbols indicate large fruits. Species names are shown for major (roman letter) and complementary species (italic letter) as follows: AcA, *Actinidia arguta*; ALa, *Actinodaphne lancifolia*; ALo, *A. longifolia*; AmC, *Ampelopsis cantoniensis*; ArC, *Ardisia crenata*; CeO, *Celastrus orbiculatus*; CiJ, *Cinnamomum japonicum*; CIJ, *Cleyera japonica*; CoB, *Cornus brachypoda*; CoC, *C. controversa*; DaM, *Daphniphyllum macropodum*; DI, *Damnanthus indicus*; DiM, *Diospyros morrisiana*; ElG, *Elaeagnus glabra*; EuJ, *Eurya japonica*; FE, *Ficus erecta*; FS, *F. sarmentosa* var. *nipponica*; IdP, *Idesia polycarpa*; IlG, *Ilex goshiensis*; III, *I. integra*; LJ, *Lasianthus japonicus*; MaJ, *Maesa japonica*; MeD, *Menispermum dauricum*; MR, *Meliosma rigida*; NA, *Neolitsea aciculata*; PaT, *Parthenocissus tricuspidata*; Pe, *Persea japonica* and *P. thunbergii*; PoM, *Podocarpus macrophyllus*; PrJ, *Prunus jamasakura*; SP, *Symplocos prunifolia*; TaY, *Taxillus yadoriki*; TeG, *Ternstroemia gymnanthera*; ZA, *Zanthoxylum ailanthoides*. Data for *P. japonica* and *P. thunbergii* was combined.

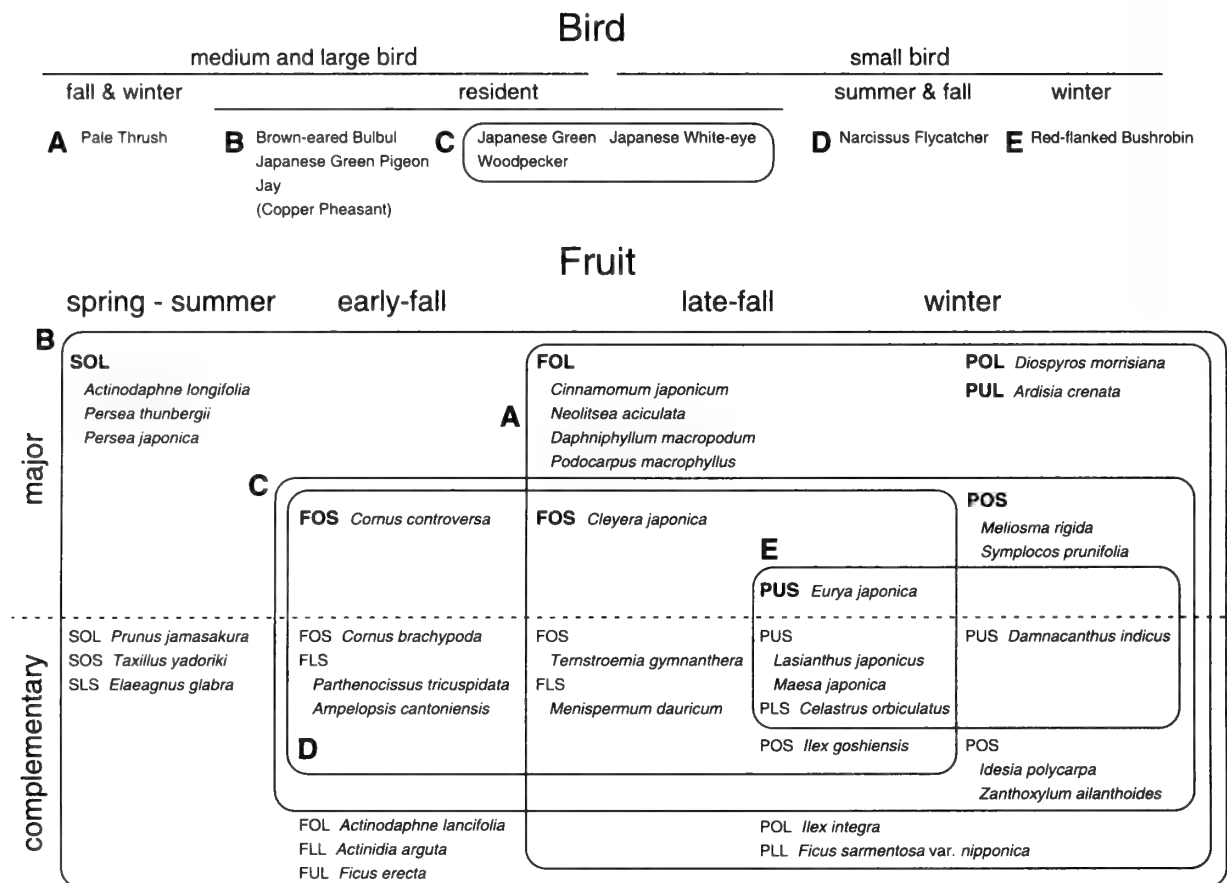


Fig. 6. Relationship patterns between fruit and bird species. Letters A to E indicate the ranges of fruits that are considered to be eaten by the birds with the same letter. Major and complementary fruit species are arranged vertically, and phenological patterns are arranged horizontally. Plant types are represented by three letters as follows: the first letter indicates phenological type (S, summer; F, fall; P, persistent), the second letter indicates growth form (O, overstory; U, understory; L, liana), and the last letter indicates fruit size (L, large; S, small). For example, SOL indicates summer-overstory-large type. Of the birds, Copper Pheasant (in parenthesis) is a seed predator.

Three tree species producing SOL fruits were major species in spring and summer (Fig. 6). Two dominant canopy species (*Persea thunbergii* and *P. japonica*) and a subcanopy species (*Actinodaphne longifolia*) showed abundant population (Fig. 5a). Most frugivorous birds eat mainly insects during the spring and summer, while Brown-eared Bulbul and Japanese Green Pigeon frequently eat fruits in these seasons (Haneda & Kobayashi 1967; Kiyosu 1978; Moriyama et al. 1985). Growth form and fruit sizes of SOL species are available for Brown-eared Bulbul and Japanese Green Pigeon. Both species ate many species of overstory fruits (Table 1). The Brown-eared Bulbul was a generalist with respect to fruit size (Fig. 4). Although 81% of the fruit species in the diet of Japanese Green Pigeon were small ones, this pigeon is known to eat the SOL fruits of *Prunus ja-*

masakura (Kiyosu 1978). *P. jamasakura*, a deciduous canopy species with a low population density (0.25 individuals ha⁻¹), was also considered an important food for birds, because the number of fruits in the 54-months seed rain equalled that of *A. longifolia* (Fig. 5a), and the bird-dispersed seed rain was observed every year. A summer-overstory-small (SOS) type woody epiphyte *Taxillus yadoriki* and a summer-liana-small (SLS) type *Elaeagnus glabra* provided the fruits from April to June that compensated for the lack of SOL fruit in early spring (Fig. 1). *P. jamasakura*, *T. yadoriki* and *E. glabra* were considered complementary species (Fig. 6).

Four FOL, two FOS, and one PUS fruits were major species in fall (Fig. 6). Two subcanopy species (*Cinnamomum japonicum* and *Neolitsea aciculata*) were abundant FOL species (Fig. 5a). A canopy tree

Daphniphyllum macropodum and a conifer *Podocarpus macrophyllus* were common FOL species that contributed large number of fruits in the seed rain (Fig. 5a). A dominant subcanopy tree *Cleyera japonica* was the most abundant FOS species, both in population and in seed rain (Fig. 5a). A deciduous tree *Cornus controversa* was a common FOS species that contributed more than 6,000 fruits in the seed rain (Fig. 5a). A small tree *Eurya japonica* was an abundant PUS species (Fig. 5c). The demand for fruits in the fall is great, because this is the season when many bird species in the temperate zone shift their food habits from animal food to vegetable matter (Sorensen 1981; Herrera 1984). Due to the abundance of FOL, FOS, and PUS species in the study site (Fig. 5), fruits are abundant and available for various birds in the fall. FOL fruits are consumed mainly by birds that eat a wide range of fruit sizes, such as Brown-eared Bulbul and Pale Thrush. Bird species with a wide range of body size consume FOS and PUS fruits.

Of seven major plant species in fall (Fig. 6), only one FOS species *Cornus controversa* provided a considerable quantity of fruit in early fall (Fig. 2). Large numbers of *C. controversa* seeds were collected in traps (>500 for all seeds, >200 for bird-dispersed seeds) in every year from 1992 to 1995. *C. controversa* fruits were available in early fall in 1992, 1993, and 1995; however, most were eaten by birds before August in 1994. The fluctuation in the availability of *C. controversa* fruits indicates that complementary species are necessary to maintain a stable supply of fruit for birds in early fall. Six species of five types were considered as complementary species in early fall (Fig. 6). A subcanopy tree *Actinodaphne lancifolia* and a liana *Actinidia arguta* were common FOL and FLL species fruiting in early fall, respectively (Fig. 2, Fig. 5a, b). A deciduous tree producing FOS fruit *Cornus brachypoda*, a small tree *Ficus erecta* (fall-understory-large (FUL) fruit), and two species of liana, *Parthenocissus tricuspidata* and *Ampelopsis*, (fall-liana-small (FLS) fruits), contributed more than 100 fruits in the seed rain, although their populations were small (Fig. 5a, b, c). Large numbers of seeds of these four species were dispersed by birds in early fall (Fig. 2).

Many persistent species fruit in late fall, and 35 species (17 fall species and 18 persistent species) contributed to a peak in the bird-dispersed seed rain. Of seven major plant species in fall (Fig. 6), seed rain of six species peaked in late fall (Fig. 2). Therefore,

the number of major species is relatively large in late fall, as compared to the number in early fall. Coincidentally, the number of frugivorous birds in lucidophyllous forests peaks in late fall (Noma & Yumoto 1997). Complementary fruit species are also available at that time. Eight species of seven types were considered as complementary species in late fall (Fig. 6). A subcanopy FOS species *Ternstroemia gymnanthera*, a liana PLL species *Ficus sarmentosa* var. *nipponica*, and two shrub PUS species (*Maesa japonica* and *Lasianthus japonicus*) were common species fruiting in late fall (Fig. 2, Fig. 3, Fig. 5a, b, d). A subcanopy POL species *Ilex integra*, a subcanopy POS species *I. goshiensis*, a persistent-liana-small (PLS) species *Celastrus orbiculatus*, and a liana FLS species *Menispermum dauricum* contributed more than 100 fruits in the seed rain, although their populations were small (Fig. 5a, b). Bird-dispersed seed rain of these four species peaked in late fall (Fig. 2, Fig. 3).

Five species of persistent fruits were major species in winter (Fig. 6). *Eurya japonica*, a major species in fall, had a second peak of bird-dispersed seed rain in winter (Fig. 3). Two subcanopy POS species (*Meliosma rigida* and *Symplocos prunifolia*), a canopy POL species *Diospyros morrisiana*, and a shrub PUL species *Ardisia crenata* were common species which contributed more than 100 fruits in the seed rain (Fig. 5a, d). Persistent fruits that have not been consumed in late-fall are an important food resource for frugivorous birds in winter. PUS fruits, in particular, are important for Red-flanked Bushrobin, a small bird that visits in winter and prefers fruits in the understory. PUL and POL fruits are consumed mainly by medium and large birds, such as Brown-eared Bulbul and Pale Thrush. Seven complementary species of persistent fruits in late fall (Fig. 6) may improve the total fruit availability in winter, as considerable amounts of these fruits remain during this season. In addition, three species were considered complementary species in winter. These were a PUS species *Damnacanthus indicus*, an abundant shrub (Fig. 5d), and two deciduous POS species (*Zanthoxylum ailanthoides* and *Idesia polycarpa*) both of which contributed more than 100 fruits in the seed rain, although their populations were small (Fig. 5a).

2) Overview of fruit-bird interactions

We classified the relationships of fruits and birds into five patterns according to the composition of major and complementary fruits in the study site (Fig.

6). Among the resident birds recorded, three species are considered to be seed dispersal agents of most fruit types (B in Fig. 6). The Brown-eared Bulbul is a major dispersal agent in lucidophyllous forests, where it is abundant throughout the seasons (Sako et al. 1971; Kawaji 1988; Eguchi et al. 1989; 1992; Noma & Yumoto 1997) and eats fruits of a wide range of sizes (Fig. 4). Fukui (1995) confirmed the efficiency of the Brown-eared Bulbul as a seed dispersal agent. In the study site, 57 (51%) of 111 endozoochorous species and 14 (82%) of 17 fruit types were found in the Brown-eared Bulbul's diet. Thus, it appears that most types of fruit are eaten and dispersed by this species. Both the Japanese Green Pigeon and the Jay are resident frugivorous birds. These species are possible be important dispersal agents in all seasons, however, the fruit size and growth form preference of the Japanese Green Pigeon may restrict the range of fruits eaten and dispersed by this species compared with the Brown-eared Bulbul.

Fruits of 21 plant species in the study site were found in the diet of the Copper Pheasant, giving it the second most diverse fruit diet after the Brown-eared Bulbul (Table 1). The Copper Pheasant is, however, capable of digesting many different kinds of seeds. Ogasawara (1968) found intact seeds in its crop, but not in the gizzard. Thus, the Copper Pheasant is presumably a seed predator rather than a seed disperser, especially, of poorly protected seeds such as those of the Lauraceae.

Five other species of birds are also considered as important seed dispersal agents, although the fruits that they eat are limited by growth form, fruiting season, or fruit size. Pale Thrush (Turdidae) is one of the most important dispersal agents in late fall and winter. The Turdidae includes many seed-dispersing species found in various vegetation types in the temperate zone (Karasawa 1978; Thomson & Willson 1979; Sorensen 1981; Herrera 1984; Skeate 1987; Debussche & Isenmann 1989; Jordano 1993). The Pale Thrush population peaks in November and many individuals overwinter in lucidophyllous forests (Noma & Yumoto 1997). This study showed that the Pale Thrush is a generalist concerning fruit size and growth form (Table 1, Fig. 4). Therefore, the Pale Thrush is thought to disperse seed of most fruit types available in late fall and in winter (A in Fig. 6). Small birds, such as Japanese White-eye, Narcissus Flycatcher, and Red-flanked Bushrobin, eat small fruits primarily, and the medium-sized Japanese Green Woodpecker also tends to prefer small fruits (C, D, E

in Fig. 6). These birds seemed to be important dispersal agents for small fruits. Since Narcissus Flycatcher is insectivorous in summer (Chiba et al. 1972; Kiyosu 1978) and absent from the study site in winter, this species eats fruits mainly in fall (D in Fig. 6). The Red-flanked Bushrobin, which eats understory small fruits in winter (E in Fig. 6), is the most limited agent among the major bird species contributing seed dispersal.

Therefore, eight species of birds were considered to be major species for seed dispersal in the study site. An overview of the relationships between these birds and various types of fruits revealed five patterns (Fig. 6). The importance of other common frugivorous birds in the study site (Table 1) as dispersal agents remains unknown. They may contribute to seed dispersal to some extent. The Masked Grosbeak, however, is a seed predator rather than a dispersal agent, because it is a species of finch (Fringillidae), which are mashers of fruits and crush seeds in their bills (Herrera 1984; Levey 1987).

3) Key species

This study described interspecific relation patterns of fruit-bird interactions in the Aya lucidophyllous forest (Fig. 6). We considered an irreplaceable major species to be a key species. Two species of Theaceae (*Eurya japonica* and *Cleyera japonica*) were considered to be key fruit species. Of the major fruit species, *E. japonica* was the only fruit found in all five patterns of fruit-bird relationship (A–E in Fig. 6), and *C. japonica* was the only fruit found in four patterns (A–D). The populations of those two species were the largest, and the amounts of seed rain from these species were the greatest for the persistent and fall types, respectively (Fig. 5). The annual fluctuation in fruit production by *E. japonica* and *C. japonica* is small in lucidophyllous forest (Noma 1997). Thus *E. japonica* and *C. japonica* have abundant populations, bear considerable numbers of fruit, produce fruit constantly, and are associated with a wide range of birds. No other species has such a complete set of these traits. Therefore, the fruits of *E. japonica* and *C. japonica* are considered as important food resources for most frugivorous birds. Any reduction in the number of fruiting individuals might seriously reduce the overall availability of fruits in the study site.

There was no key plant species in spring and summer. The SOL species were important food resources for Brown-eared Bulbul and Japanese Green Pigeon. However, it is still not known whether any of the

SOL species is replaceable. The fruiting periods within summer differed between two species of *Persea* and the other two species (*Actinodaphne longifolia* and *Prunus jamasakura*). The fruit production by these species showed considerable annual fluctuation and was not synchronized among species (Kominami unpubl.). Therefore, the SOL species provide fruits in turn. In spring and summer, each SOL species might be replaceable in the short term, but the complete set of these species might be necessary in the long term.

Cornus controversa was considered a key species because its fruit was the only major species in early fall. It produced the largest amount of fruits in early fall, and these were constantly available for birds. It was also included in the food of at least six species of common frugivorous birds. Therefore, *C. controversa* fruit is expected to be a popular food resource for many birds in early fall.

We did not find any key fruit species as component species in a strong relationship. Fruit-bird interactions in the study site overlapped in various ways (Fig. 6). Hence, there was no strong relationship involving birds and fruits that were independent of all other relationships as one might expect in a tropical forest area.

In the diffuse pattern of relationships seen at the study site, the abundance and generality of key species may improve the stability of food resources and of dispersal success. Some studies of temperate forests have found that a few abundant species are "key species", playing crucial roles in fruit-bird interactions (Skeate 1987; Debussche & Isenmann 1989). In our study site, an important species set composed of three key fruit species and a group of summer fruits provided continuous and familiar food for many bird species. The key fruit species in this study site are also common species in other lucidophyllous forests (Noma & Yumoto 1997; Hattori & Minamiyama 2001), and may play similar roles there.

4) Conservation of fruit-bird interactions

How do the details of the relationship patterns detected in this study contribute to the conservation of fruit-bird interactions in lucidophyllous forests? To diagnose the stability of fruit-bird interactions, it is useful to determine whether the composition of fruit types in a forest is similar to that in the study site. Observed relationship patterns in a primary lucidophyllous forest represent one fundamental pattern for lucidophyllous forests in Japan. Since there are vari-

ous lucidophyllous forest communities (Sato 1983), the species composition of each relationship, e.g., A-E in Fig. 6, is likely to differ somewhat among communities. It is important to detect differences in the overall composition of fruit types rather than in species composition. If a fruit type is absent from a lucidophyllous forest, the cause of this absence should be determined. If the absence of a type is caused by natural variation in the vegetation, management is not necessary; however, if the absence is caused by human impact, the type should be restored. In particular, a sudden decrease in key species might seriously affect fruit-bird interactions, causing a food scarcity for birds, and preventing adequate seed dispersal for plants. Therefore, monitoring the populations of key species is essential for conserving fruit-bird interactions in lucidophyllous forests.

The results of this study suggest that conservation of the overall composition of fruit types improves the stability of food resources for birds and facilitates dispersal success for the plants themselves. The frugivorous bird population and the degree of frugivory in temperate forests undergo large annual fluctuations, especially in fall and winter (Stapanian 1982; Malmberg & Willson 1988; Jordano 1993; Herrera 1998). Fruit abundance also varies markedly among years (Herrera 1984, 1998; Wheelwright 1986; Jordano 1993; Noma 1997). These fluctuations in birds and fruits may lead to an annual, unpredictable variability in the available species of the fruit-bird interaction. Insofar as endozoochorous plants are rich in fruit types, some of the types may compensate for any sudden fluctuation in the key or major species.

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Appendix 1. Disseminule form composition of higher plants in the Aya Research Site.

Growth form	EN	SY	EP	MY	AN	AU	BA	SP	Total
Number of species									
Tree	59	13	0	0	11	0	1	0	84
Canopy and subcanopy	36	11	0	0	11	0	1	0	59
Small tree	23	2	0	0	0	0	0	0	25
Shrub	27	0	0	0	0	0	2	0	29
Liana	21	0	0	0	4	0	0	0	25
Woody epiphyte	1	0	0	0	0	1	0	0	2
All woody plants	108	13	0	0	15	1	3	0	140
Herb	3	0	1	1	36	0	2	0	43
Fern	0	0	0	0	0	0	0	20	20
All plants	111	13	1	1	51	1	5	20	203

EN, endozoochore dispersed by frugivores; SY, synzoochore dispersed by food hoarding; EP, epizoochore carried on the outside of animals; MY, myrmecochore dispersed by ants; AN, anemochore dispersed by wind; AU, autochore dispersed by the plant itself; BA, barochore dispersed by weight only; SP, spore.

Appendix 2. Traits and abundance of 111 endozoochorous plant species in the Aya Research Site.

Family	Species	Phenology ^a	Growth ^c form	Size ^d	Seed ^e size	Fruit ^e size	No of ^f individuals	No of ^g quadrats	No of ^h fruits	Role ⁱ
Actinidiaceae	<i>Actinidia arguta</i>	F	L	L	1.3		19		98	C
Actinidiaceae	<i>Actinidia polygama</i>	F	L	L	1.1	12.1	5		1	
Anacardiaceae	<i>Rhus ambigua</i>	u	L	S	3.6		4		2	
Anacardiaceae	<i>Rhus javanica</i>	u	U	S	2.5	3.8			3	
Anacardiaceae	<i>Rhus sylvestris</i>	u	U	S	4.6	7.1			1	
Anacardiaceae	<i>Rhus trichocarpa</i>	u	U	S		4.2				
Aquifoliaceae	<i>Ilex buergeri</i>	u	O	S	2.7	6.8	1		1	
Aquifoliaceae	<i>Ilex integra</i>	P	O	L	4.1	10.1	6		166	
Aquifoliaceae	<i>Ilex latifolia</i>	u	O	S	2.4	6.8				
Aquifoliaceae	<i>Ilex macropoda</i>	u	O	S	1.9					
Aquifoliaceae	<i>Ilex rotunda</i>	P	O	S	1.3	5.6	1		17	
Aquifoliaceae	<i>Ilex goshiensis</i>	P	O	S	1.4		1		259	C
Araceae	<i>Arisaema</i> sp.	u	U	u						
Araliaceae	<i>Aralia elata</i>	u	U	S	1.3	4.0				
Araliaceae	<i>Dendropanax trifidus</i>	F	U	S	1.8	6.2	1		6	
Caprifoliaceae	<i>Lonicara hypoglauca</i>	F	L	S	2.6		1		15	
Caprifoliaceae	<i>Lonicera japonica</i>	F	L	S	2.0		1		2	
Caprifoliaceae	<i>Sambucus sieboldiana</i>	S	U	S	1.5	3.7		1	29	
Caprifoliaceae	<i>Viburnum awabuki</i>	u	O	S	3.7	5.0	1		1	
Caprifoliaceae	<i>Viburnum dilatatum</i>	u	U	S	3.9	5.5			2	
Celastraceae	<i>Celastrus orbiculatus</i>	P	L	S	2.7	4.9	3		138	C
Cephalotaxaceae	<i>Cephalotaxus harringtonia</i>	u	U	L	9.9					
Chloranthaceae	<i>Chloranthus glaber</i>	F	U	S	2.9			12	15	
Cornaceae	<i>Aucuba japonica</i>	u	U	L	9.6	11.7		1		
Cornaceae	<i>Cornus brachypoda</i>	F	O	S	3.3	4.3	6		281	
Cornaceae	<i>Cornus controversa</i>	F	O	S	4.9		14		6835	K
Ebenaceae	<i>Diospyros japonica</i>	F	O	L	6.2		7		46	
Ebenaceae	<i>Diospyros morrisiana</i>	P	O	L	5.1		25		247	M
Elaeagnaceae	<i>Elaeagnus glabra</i>	S	L	S	4.4				79	C
Elaeagnaceae	<i>Elaeagnus pungens</i>	u	U	S						
Elaeocarpaceae	<i>Elaeocarpus japonicus</i>	F	U	L	5.7				28	
Ericaceae	<i>Vaccinium bracteatum</i>	P ^b	U	S	1.0	4.5				
Euphorbiaceae	<i>Antidesma japonicum</i>	u	U	S	2.2		1		10	
Euphorbiaceae	<i>Daphniphyllum macropodum</i>	F	O	L	5.8	9.8	26		946	M
Euphorbiaceae	<i>Daphniphyllum teijsmanni</i>	F ^b	O	L	5.5	7.7	8			
Euphorbiaceae	<i>Mallotus japonicus</i>	u	O	S	3.2	5.2			2	
Flacourtiaceae	<i>Idesia polycarpa</i>	P	O	S	1.3	7.9	4		136	M
Flacourtiaceae	<i>Xylosma congestum</i>	P	U	S	2.6			1	20	
Lardizabalaceae	<i>Akebia trifoliata</i>	F	L	u	3.9				1	
Lardizabalaceae	<i>Stauntonia hexaphylla</i>	F	L	L	4.7	44.2				
Lauraceae	<i>Actinodaphne lancifolia</i>	F	O	L	5.1		20		68	C
Lauraceae	<i>Actinodaphne longifolia</i>	S	O	L	7.7	10.8	128		76	M
Lauraceae	<i>Cinnamomum camphora</i>	u	O	L	5.9	10.1	1		8	
Lauraceae	<i>Cinnamomum japonicum</i>	F	O	L	6.6	7.6	149		645	M
Lauraceae	<i>Lindera erythrocarpa</i>	u	O	S	4.5	5.7			4	
Lauraceae	<i>Neolitsea aciculata</i>	F	O	L	5.8		105		399	M
Lauraceae	<i>Neolitsea sericea</i>	P	U	L	7.6		6		21	
Lauraceae	<i>Persea japonica</i>	S	O	L	9.3		356		2213 ⁱ	M
Lauraceae	<i>Persea thunbergii</i>	S ^b	O	L	9.4	10.6	165		–	M
Leguminosae	<i>Euchresta japonica</i>	u	U	L	7.1	9.1		15		

Appendix 2. (Continued)

Family	Species	Phenology ^a	Growth form ^c	Size ^d	Seed size ^e	Fruit size ^e	No of ^f individuals	No of ^g quadrats	No of ^h fruits	Role ^j
Liliaceae	<i>Smilax china</i>	u	U	S	3.7	8.4		2		
Loganiaceae	<i>Gardneria nutans</i>	u	L	L					1	
Loranthaceae	<i>Taxillus yadoriki</i>	S	O	S					519	C
Magnoliaceae	<i>Michelia compressa</i>	u	O	L	6.6	7.6	2			
Meliaceae	<i>Melia azedarach</i>	u	O	L	7.4	13.0				
Menispermaceae	<i>Menispermum dauricum</i>	F	L	S	4.6				405	
Menispermaceae	<i>Stephania japonica</i>	u	L	S	4.4				1	
Moraceae	<i>Broussonetia kaempferi</i>	S	L	u	1.4				4	
Moraceae	<i>Ficus erecta</i>	F	U	L	1.1	14.5	8		125	C
Moraceae	<i>Ficus sarmentosa</i> var. <i>nipponica</i>	P	L	L	1.0		14		9	C
Moraceae	<i>Maclura cochinchinensis</i> var. <i>gerontogea</i>	u	L	L						
Moraceae	<i>Morus bombycis</i>	u	U	S	1.1	7.6			1	
Myricaceae	<i>Myrica rubra</i>	S ^b	O	L	6.4	13.5			17	
Myrsinaceae	<i>Ardisia crenata</i>	P	U	L	5.0			39	886	M
Myrsinaceae	<i>Ardisia japonica</i>	u	U	S	4.3	6.9			1	
Myrsinaceae	<i>Maesa japonica</i>	P	U	S	0.5	5.0		270	30	C
Myrsinaceae	<i>Myrsine seguinii</i>	P ^b	U	L						
Myrtaceae	<i>Syzygium buxifolium</i>	F ^b	U	L	5.4	8.0	3		3	
Oleaceae	<i>Ligustrum japonicum</i>	u	U	S	3.2					
Oleaceae	<i>Osmanthus insularis</i>	u	O	L			2		3	
Piperaceae	<i>Piper kadsura</i>	u	L	S	2.6					
Podocarpaceae	<i>Podocarpus macrophyllus</i>	F	O	L	9.6		13		1836	M
Rhamnaceae	<i>Berchemia racemosa</i>	u	L	S	2.8		1			
Rosaceae	<i>Prunus jamasakura</i>	S	O	L	5.5		1		95	M
Rosaceae	<i>Prunus spinulosa</i>	u	U	L	5.2				2	
Rosaceae	<i>Rubus buergeri</i>	u	U	S	1.5	6.5		4		
Rosaceae	<i>Rubus crataegifolius</i>	S	U	L	1.2	11.8			2	
Rosaceae	<i>Rubus hirsutus</i>	u	U	L	1.0	14.3				
Rosaceae	<i>Rubus minusculus</i>	u	U	u	0.9			3		
Rosaceae	<i>Rubus palmatus</i>	u	U	L	1.2	11.2				
Rosaceae	<i>Rubus sieboldii</i>	u	U	L	1.2					
Rubiaceae	<i>Damnacanthus indicus</i>	P	U	S	2.3	4.2		131	14	C
Rubiaceae	<i>Lasianthus japonicus</i>	P	U	S	1.6			43	59	C
Rubiaceae	<i>Paederia scandens</i> var. <i>mairei</i>	P	U	S	3.4	5.5			23	
Rubiaceae	<i>Randia cochinchinensis</i>	u	U	S						
Rutaceae	<i>Evodia meliaefolia</i>	P	U	S	2.0	2.0			86	
Rutaceae	<i>Skimmia japonica</i>	u	U	S	4.3	8.4		14	2	
Rutaceae	<i>Zanthoxylum ailanthoides</i>	P	O	S	2.8	2.9	3		804	C
Sabiaceae	<i>Meliosma rigida</i>	P	O	S	4.9		26		496	C
Schisandraceae	<i>Kadsura japonica</i>	P	L	S	3.5	5.9			3	
Simaroubaceae	<i>Picrasma quassioides</i>	S	O	S	3.7				54	
Symplocaceae	<i>Symplocos glauca</i>	u	U	L	6.2		2			
Symplocaceae	<i>Symplocos lancifolia</i>	u	U	S	3.4				10	
Symplocaceae	<i>Symplocos lucida</i>	u	U	S	4.7	7.7			1	
Symplocaceae	<i>Symplocos myrtacea</i>	F	U	S	3.0		1		66	
Symplocaceae	<i>Symplocos prunifolia</i>	P	O	S	2.8		17		154	C
Symplocaceae	<i>Symplocos theophrastaefolia</i>	P	U	S	3.9	5.0	1		75	

Appendix 2. (Continued)

Family	Species	Phenology ^a	Growth ^c form	Size ^d	Seed ^e size	Fruit ^e size	No of ^f individuals	No of ^g quadrats	No of ^h fruits	Role ^j
Theaceae	<i>Cleyera japonica</i>	F	O	S	2.1	7.3	1069		7706	K
Theaceae	<i>Eurya japonica</i>	P	U	S	1.2	5.8	139		1115	K
Theaceae	<i>Ternstroemia gymnanthera</i>	F	O	S			15		41	C
Thymelaeaceae	<i>Daphne Kiusiana</i>	u	U	S	3.8	6.6		3	1	
Ulmaceae	<i>Aphananthe aspera</i>	u	O	L	7.1	10.1			1	
Urticaceae	<i>Villebrunea frutescens</i>	u	U	S				3		
Verbenaceae	<i>Callicarpa japonica</i>	u	U	S	1.5	3.5		1		
Verbenaceae	<i>Callicarpa mollis</i>	P	U	S	1.7			6	22	
Verbenaceae	<i>Clerodendron trichotomum</i>	u	U	S	4.4	6.4				
Verbenaceae	<i>Premna japonica</i>	S	U	S	2.9		8		28	
Vitaceae	<i>Ampelopsis brevipedunculata</i>	u	U	S	3.4	5.8				
Vitaceae	<i>Ampelopsis cantoniensis</i>	F	L	S	2.8				359	C
Vitaceae	<i>Parthenocissus tricuspidata</i>	F	L	S	3.3		2		537	C
Vitaceae	<i>Vitis flexuosa</i>	u	L	S			1			

^a Phenological pattern of fruiting and dispersal: S, summer type; F, fall type; P, persistent type; u, unknown.

^b The type is considered by the phenological patterns reported in Noma & Yumoto (1997).

^c O, overstory; U, understory; L, liana.

^d Fruit size class: L, large; S, small; u, unknown.

^e Mean shorter diameters (mm) of seed and fruit. Only original data are shown.

^f Number of individuals with DBH of >5 cm in the 4-ha plot. A blank indicates no record in the tree census of this study.

^g Number of quadrats where the shrub and herb species was observed among 441 quadrats in the 4-ha plot. A blank indicates no record in the quadrats of this study.

^h Total number of fruits fallen into 263 traps (total cover 153 m²) in 54 months, calculated from the total number of seeds fallen into traps and the number of seeds per fruit.

ⁱ The data of *Persea japonica* and *P. thunbergii* are combined.

^j Role in fruit-bird interaction: K, key species; M, major species; C, complementary species.

Fruiting of fleshy-fruited plants and abundance of frugivorous birds: Phenological correspondence in a temperate forest in central Japan

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Abstract We investigated the seasonal correspondence between the fruiting phenology of fleshy-fruited plants and the abundance of frugivorous birds, in a temperate forest, in central Japan. The majority of fleshy fruits ripened in the fall when frugivorous birds were most abundant. This correspondence occurred earlier than in a warm temperate forest, located in southern Japan; these relationships in East Asia coincide with those of the temperate regions of North America and Europe. We also examined whether the abundance of frugivorous birds led to profitable effects for seed dispersal among fleshy-fruited plants. The Brown-eared Bulbul *Hypsipetes amaurotis* was considered to be an important seed disperser for many fleshy-fruited plants because of its high frequency of occurrence throughout the fruiting season, and its large gape size, which allowed it to swallow all sizes of fruits found at the study site. Although numerous Brown-eared Bulbuls and other frugivorous birds were present in the fall, fruit removal rates in fall-fruiting species were not always higher than in summer-fruiting species. The abundance of frugivorous birds alone could therefore not adequately explain the concentrated fruiting phenology among fleshy-fruited plants.

Key words Fleshy-fruited plant, Frugivorous bird, Fruit removal rate, Fruiting phenology

The relationship between the fruiting phenology of fleshy-fruited plants and their dispersal agents has been described at the community level in various regions (e.g., Thompson & Willson 1979; Stiles 1980; Sorensen 1981; Herrera 1984; Izhaki & Safriel 1985; Skeate 1987; Loiselle & Blake 1991; Debussche & Isenmann 1992; French 1992; Noma & Yumoto 1997). Fruiting periods that correspond to seasonal variation in the abundance of dispersal agents have been identified as one of the characteristic events of temperate regions. In North America, this correspondence has been examined in different climatic regions. The fruiting periods of many fleshy-fruited plants in cool temperate forests are generally concentrated in the fall, when a large number of frugivorous birds migrate south (Thompson & Willson 1979; Stiles 1980; Stapanian 1982). Fruiting periods in a warm southern temperate forest, however, were post-

poned to the winter, when large populations of frugivorous birds arrived to overwinter (Skeate 1987). Similar relationships have also been reported in Europe (Herrera 1984), and variations in the dates of maximum fruit availability among communities situated along latitudinal gradients coincide with those of maximum abundance of frugivorous birds (Fuentes 1992). In East Asia, Noma and Yumoto (1997) found a close correspondence between the fruiting periods of many fleshy-fruited plants and the fluctuation of frugivorous birds in a warm temperate forest, in southern Japan. This correspondence was similar to previous reports from lower latitudes in North America and Europe, however, no detailed comparison with other regions has been conducted in East Asia.

We examined the possibility that efficient seed dispersal may cause the fruiting period of a fleshy-fruited plant to coincide with the fall migration and overwintering of many frugivorous birds. Abundant dispersal agents may cause higher rates of fruit removal and constitute, therefore, a selective influence

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on the fruiting phenology of fleshy-fruited plants. Contrary to this hypothesis, however, not all species, whose fruits ripen when frugivorous birds are plentiful, show evidence of higher fruit removal rates. In fleshy-fruited plants that have low quality fruits, the fruits persist on the trees for a long time and are dispersed less efficiently (Stiles 1980; Kominami 1987).

The objective of our research was to examine the correspondence between the fruiting periods of various fleshy-fruited plants and seasonal variation in the abundance of frugivorous birds in a temperate forest, in central Japan. In particular, it was thought that a comparison with the findings from a warm temperate forest in southern Japan (Noma & Yumoto 1997) would help to explain the mechanisms of seed dispersal by frugivorous birds in East Asia from a phenological point of view. We also examined whether frugivorous birds present during the fruiting periods of fleshy-fruited plants would have a large gape size enough to swallow fruits whole. Frugivorous birds with a small gape can swallow only small fruits, while those with a large one can swallow fruits of various sizes (Wheelwright 1985; Noma & Yumoto 1997). Finally, we tested the hypothesis that fruiting during a period when frugivorous birds are most abundant leads to stable and higher fruit removal. We also discuss profitable fruiting periods for seed dispersal among fleshy-fruited plants.

METHODS

1) Study site

The study site was located at the foot of Mt. Kakuda (482 m) in Niigata Prefecture, central Japan (37°46'N, 138°50'E). According to the Niigata Meteorological Observatory, the mean annual temperature and precipitation are 13.5°C and 1,776 mm, respectively. The elevation is approximately 100 m a.s.l. The major canopy species are *Quercus serrata* and *Pinus densiflora*, whereas the shrub layer is composed mainly of *Eurya japonica*, *Viburnum dilatatum*, and *Aucuba japonica* var. *borealis*. Both cool and warm temperate forest species are found at the study site.

2) Frugivorous birds

The population and species composition of birds were recorded by the line-census method from May 1995 to April 1997. A census route approximately 1.5 km long was established along a path through the study site. We walked along the census route for three

hours just after sunrise and recorded all birds observed within 25 m of both sides of the line. The census was usually conducted once a week, but in the fall, when bird abundance fluctuated dramatically, it was conducted three times a week. Due to inclement weather, the frequency of observations was reduced in the winter. The literature (Kiyosu 1978) and direct observations served to establish whether observed bird species were frugivorous (see Appendix 1).

3) Fleshy-fruited plants

We monitored the flowering and fruiting phenology of 51 woody plant species that bore fleshy fruits (see Appendix 2). During the same period that birds were censused, five individual plants of each species were tagged along the census route, and their phenological traits, such as flowering, fruiting, and fruit disappearance, were recorded once a week. The flowering and fruiting periods of each species were defined in terms of the number of days from the first flowering and fruiting to the disappearance of all flowers and fruits on the tagged plants. From these observations of fruiting phenology, the 51 species were classified into three fruiting types; summer-, fall-, or spring-fruiting species (see Appendix 2).

Fruit removal from the six principal species of each fruiting type was examined for three consecutive years from 1996 to 1998. *Broussonetia kazinoki* (Moraceae), *Prunus apetala* ssp. *pilosa* (Rosaceae), and *Sambucus racemosa* ssp. *sieboldiana* (Caprifoliaceae) were summer-fruiting species and *Eurya japonica* (Theaceae), *Viburnum dilatatum*, and *V. wrightii* (Caprifoliaceae) were fall-fruiting species. Fruit removal rates were examined in the following two ways. In 1996, four to 12 individuals of each species were randomly selected and their fruits were counted once or twice every two weeks under natural conditions. We also selected several individuals from each species and covered their inflorescences with nylon nets to eliminate fruit consumption by birds. Fruits that dropped off naturally were caught within the nets and counted. The difference between the number of fruits that disappeared under natural conditions and the numbers on the netted plants was regarded as the number of fruits removed by birds. In 1997 and 1998, we again selected three to five individuals of the same plant species and set up seed traps underneath them. The number of fruits on the plants and the number of fruits that fell into the seed traps were recorded once or twice every two weeks. The difference between the two fruit counts was con-

sidered to be the number of fruits removed by birds.

We measured the size of 30 fruits selected randomly from the sample species. Gape sizes of frugivorous birds were recorded from the literature (Noma & Yumoto 1997).

4) Data analysis

Seasonal differences in the mean number of frugivorous bird species counted in each census were analyzed using Tamhane's multiple comparison, and differences in the mean species numbers were tested by season using Bonferroni's multiple comparison. The relationship between frugivorous bird abundance and the number of fleshy-fruited plant species with ripe fruits was investigated using Kendall's rank correlation test. For the above analyses, census data from two consecutive years were combined. Fruit removal rates in summer-fruited species were compared using a t-test to detect any differences between study years, whereas removal rates in fall-fruited species were tested with a Kruskal-Wallis test.

RESULTS

1) Seasonal variation in the abundance of frugivorous birds

Of the 63 bird species that we observed during the monitoring periods, 24 were frugivorous. Of these frugivorous species, nine were residents while the other 15 were migrants. The population of frugivorous birds was stable throughout the summer months (Fig. 1). Brown-eared Bulbuls *Hypsipetes amaurotis* were observed most frequently, while the second most observed species was the Japanese White-eyes *Zosterops japonicus*. These two species accounted for >80% of the total population of frugivorous birds recorded during the summer. The population of frugivorous birds increased rapidly in the early fall. The first peak in numbers occurred in mid-September in 1995, and in early October in 1996, and this peak was due mainly to the increase of Japanese White-eyes (Fig. 2). The second peak in both study years occurred around late October, when migratory winter birds such as Dusky Thrushes *Turdus naumanni* and Pale Thrushes *T. pallidus* began to reach the study site (Fig. 2). The Brown-eared Bulbul was observed frequently from September to November (Fig. 2). The total population of the Brown-eared Bulbul and the Japanese White-eye reached over 70% of the total population of frugivorous birds recorded during the fall. The mean number of frugivorous birds counted

during each census was higher in the fall than in the other seasons (Fig. 3). The population of frugivorous birds decreased in December and remained low

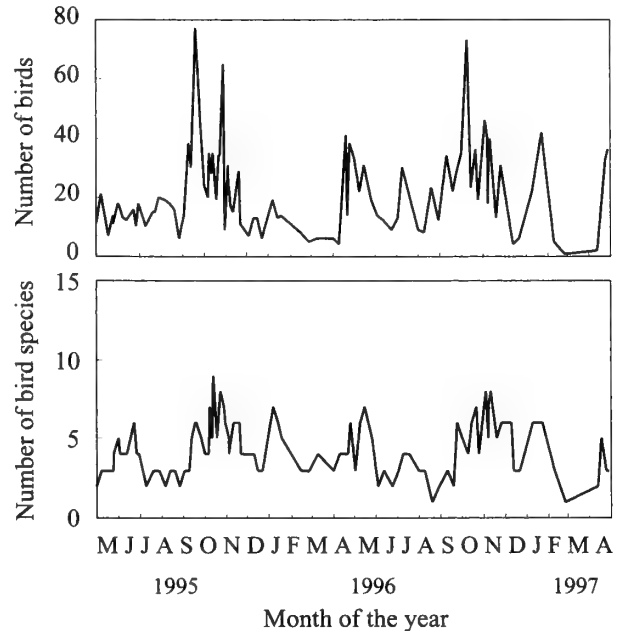


Fig. 1. Seasonal variation in the number of individuals and species of frugivorous birds recorded along a census route between May 1995 and April 1997.

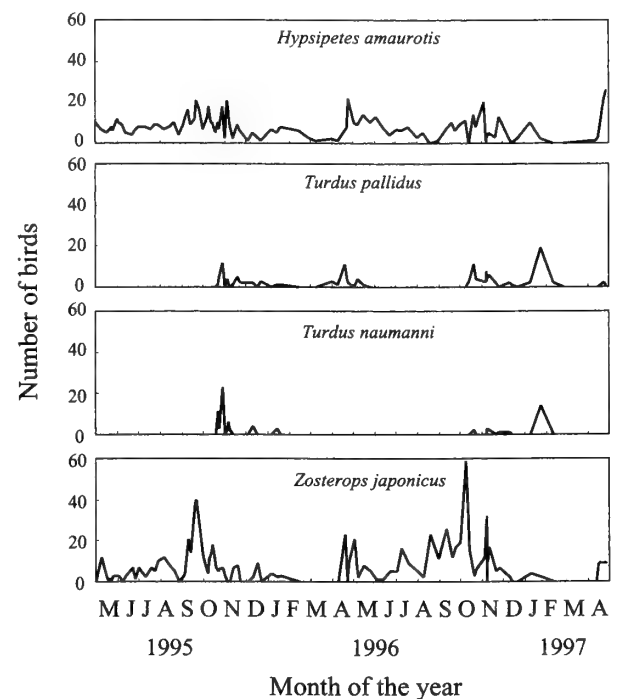


Fig. 2. Seasonal variation in the number of individuals of the principal frugivorous birds recorded along a census route between May 1995 and April 1997.

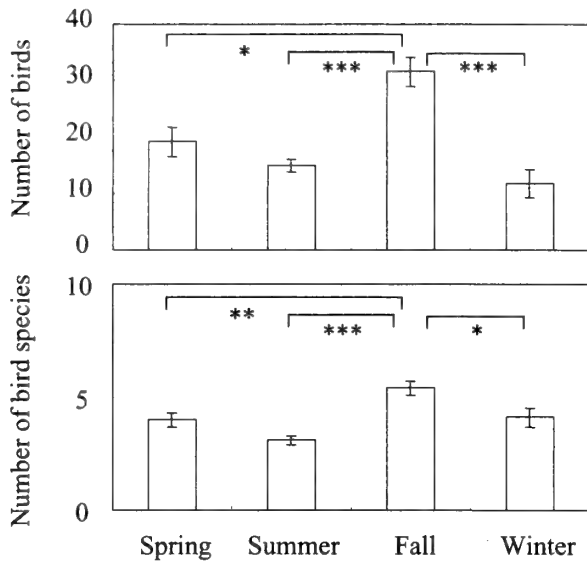


Fig. 3. Seasonal differences in the mean number of individuals and species of frugivorous birds recorded during each census (\pm SE). The combined census data for two consecutive years were divided into four categories: Spring (March–May), Summer (June–August), Fall (September–November), Winter (December–February). The number of individuals and species of birds were compared between the categories using Tamhane's and Bonferroni's multiple comparison test, respectively. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

throughout the winter months. One notable exception was a large flock of Dusky and Pale Thrushes observed in the study site in late January 1997. In mid April, the number of birds began to increase again. The dominant species were the Brown-eared Bulbul and the Japanese White-eye, which accounted for 78% of the total population of frugivorous birds observed during the spring. Seasonal variation in the number of frugivorous bird species showed a similar pattern to that of individuals (Fig. 1). The mean number of species of frugivorous birds counted during each census was higher in the fall than in the other seasons (Fig. 3).

2) Phenology of fleshy-fruited plants

The flowering periods of fleshy-fruited plants were concentrated in the period from May to July, and fruiting periods also showed a notable seasonality (Fig. 4). The number of fleshy-fruited plant species with ripe fruits fluctuated slightly during the summer, however, it increased rapidly in early September and reached a peak during late October and mid-November (Fig. 4). Thereafter, the number of fruiting species decreased gradually in late November and re-

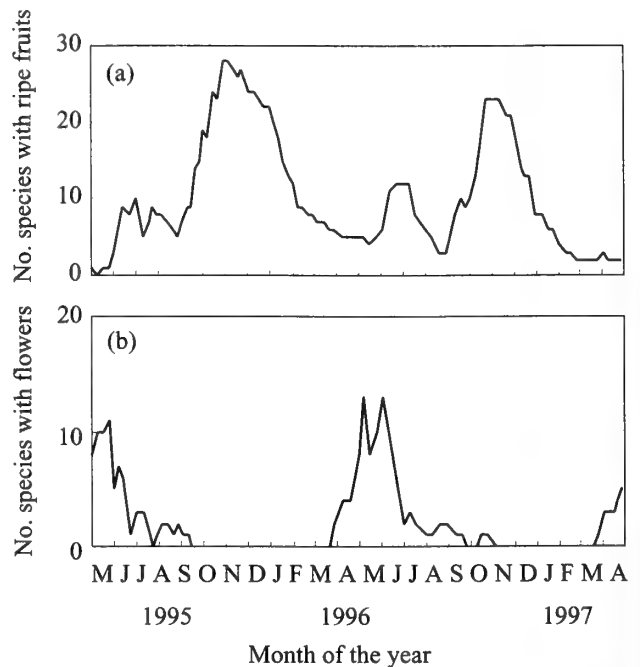


Fig. 4. Seasonal variation in the number of fleshy-fruited plant species that bore ripe fruits (a) and flowers (b) between May 1995 and April 1997.

mained low from late winter to spring. We found that the number of fruiting species and the number of frugivorous birds were significantly correlated (Kendall's rank correlation test, $\tau = 0.19$, $N = 75$, $P = 0.02$); numbers of bird species were also correlated to the number of fruiting species ($\tau = 0.39$, $N = 75$, $P = 0.00$).

Of the 51 plant species investigated, 18 were defined as summer-fruited species. Fruits of the summer-fruited species ripened soon after flowering, and almost all such fruits disappeared before the fall. Fruits of several species (*Prunus apetala* ssp. *pilosa*, *Rubus palmatus* var. *coptophyllus*, and *R. hirsutus*) began to ripen around late May. Fruits of the 32 fall-fruited species ripened from September to November, when frugivorous birds were abundant. More than 60% of the fleshy-fruited plant species in the study site belonged to this fruiting type. Several species maintained intact fruits during midwinter. The only spring-fruited species was *Aucuba japonica* var. *borealis*. Although most fleshy-fruited plants produced fruits in the fall or summer, a few fruits of *A. japonica* var. *borealis* began to ripen in late November, as the abundance of frugivorous birds decreased gradually. The majority of the fruits ripened in late March, and almost all fruits had disappeared

Table 1. Fruit removal rates in six fleshy-fruited plant species.

	1996	1997	1998	P
Summer-fruited species				
<i>Prunus apetala</i> ssp. <i>pilosa</i>	85.5±3.7 (N=10)	65.0±13.4 (N=5)	...	NS
<i>Sambucus racemosa</i> ssp. <i>sieboldiana</i>	81.5±7.3 (N=6)	76.7±7.5 (N=5)	...	NS
<i>Broussonetia kazinoki</i>	32.1±5.6 (N=12)	31.1±11.4 (N=5)	...	NS
Fall-fruited species				
<i>Eurya japonica</i>	75.8±10.6 (N=10)	16.4±10.0 (N=4)	71.4±8.8 (N=5)	<0.05
<i>Viburnum dilatatum</i>	63.9±6.1 (N=9)	19.2±9.9 (N=4)	20.1±8.5 (N=5)	<0.01
<i>V. wrightii</i>	49.9±18.0 (N=4)	32.8±3.4 (N=3)	31.4±2.5 (N=5)	NS

¹ Figures are means ± SE.

² Fruit removal rates of the summer- and fall-fruited species were compared with a t-test and a Kruskal–Wallis test, respectively.

³ NS=no significant difference ($P>0.05$); ... =no observations.

prior to fruit production of the summer-fruited species.

3) Fruit removal by frugivorous birds

Mean fruit sizes of the summer- and fall-fruited species were 8.4 ± 2.1 mm ($N=11$) and 5.9 ± 1.8 mm ($N=26$), respectively. The gape size of the Brown-eared Bulbul, which was the frugivorous bird most often observed in summer and the second most often observed in fall, is 13.3 mm (Noma & Yumoto 1997), i.e. large enough to swallow the fruits of both fruiting types whole. The gape size of the Japanese White-eye, the second most frequently observed frugivore in summer, and the most frequent in fall, is 6.1 mm (Noma & Yumoto 1997), which is only large enough to swallow the smaller fruits of both fruiting types.

We found no significant differences in fruit removal rates among summer-fruited species (*B. kazinoki*, *P. apetala* ssp. *pilosa*, and *S. racemosa* ssp. *sieboldiana*) between the study years (Table 1). Not all fruits were removed to the same degree by frugivorous birds. *P. apetala* ssp. *pilosa* and *S. racemosa* ssp. *sieboldiana* experienced high fruit removal rates (65–86%), whereas those of *B. kazinoki* were low (31–32%) in both years. In contrast, the fall-fruited species showed different tendencies over the study years (Table 1). Fruit removal rates in *E. japonica* and *V. dilatatum* were significantly different over three consecutive years, and fluctuated widely from

16 to 76%. The fruits of *V. wrightii* were consistently removed in three consecutive years. No conspicuous differences in fruit removal rates were noticed between summer- and fall-fruited species.

DISCUSSION

The fruits of more than 60% of fleshy-fruited plants in a temperate forest in central Japan ripened in the fall, when frugivorous birds were most abundant. Noma and Yumoto (1997) found a similar correspondence during the winter in a warm temperate forest in southern Japan. These findings in latitudinally diverse regions, imply a phenological correspondence during different seasons in East Asia, a correspondence that is similar to phenomena that have been reported in North America (Thompson & Willson 1979; Skeate 1987) and Europe (Fuentes 1992).

We attempted to explain these phenological correspondences by focusing on several key seed dispersers and fleshy-fruited plants. The Brown-eared Bulbul and the Japanese White-eye are probably the main seed dispersers, as they account for 44–86% of the total population of frugivorous birds during each season. The increased population of frugivorous birds recorded in the fall can be attributed to migratory flocks of Brown-eared Bulebuls and Japanese White-eyes that breed further north. In a warm temperate

forest, in southern Japan, the winter expansion of the frugivorous bird population is primarily due to the migration of wintering populations of these two bird species (Noma & Yumoto 1997). This suggests that regardless of latitude, many fleshy-fruited plants may depend on particular bird species, such as the Brown-eared Bulbul and the Japanese White-eye, for seed dispersal. Moreover, the bulbul is a very important dispersal agent qualitatively because its gape is large enough to easily swallow fruits of various sizes. Fukui (1995) found that the Brown-eared Bulbul consumed fruits of 53 species from 24 plant families. The Japanese White-eye is probably a major seed disperser for plants that bear smaller fruits. Large thrushes, such as the Dusky Thrush and the Pale Thrush, are also important bird species that are usually observed around late October at the study site. Although populations of these thrushes are not as large as those of the Brown-eared Bulbul or the Japanese White-eye, they contribute to seed dispersal due to their timely arrival and large gape size (>10.0 mm; Karasawa 1978). Kominami (1987) inferred that the Dusky Thrush contributed much to fruit removal in *V. dilatatum* in a cool temperate forest, in northern Japan, despite the presence of other dominant species such as the Brown-eared Bulbul.

We investigated whether fruit removal was profitable in the fall when frugivorous birds were most abundant at our study site. Fruit removal rates from fleshy-fruited European plants that ripen during the migratory seasons of frugivorous birds exceeded 80% (Jordano 1982; Herrera 1984), which might attest to the effect of frugivorous bird abundance on seed dispersal. High fruit removal rates at our study site were recorded in two summer-fruiting species, *P. apetala* ssp. *pilosa* and *S. racemosa* ssp. *sieboldiana*, rather than in fall-fruiting species. Fruit removal rates in the fall-fruiting species differed greatly among species and study years. Such instability may be caused by keener competition among plant species for seed dispersers due to the concentrated fruiting of fleshy-fruited plants in the fall. The peculiar position of *A. japonica* var. *borealis*, which was the only spring-fruiting species, is very interesting in our phenological study. A few frugivorous bird species, such as the Brown-eared Bulbul, were comparatively abundant in the spring, whereas fleshy-fruited plant species with ripe fruit were scarce. The spring fruiting of *A. japonica* var. *borealis* may therefore be a phenological strategy to escape interspecific competition.

Thus, fruiting in the fall when frugivorous birds

are most abundant would not necessarily lead to profitable dispersal. Our results imply that the fruits of fleshy-fruited plants are likely to be removed efficiently during each fruiting season. A long-term and continuous study (e.g., Herrera 1998) will be required to further explain the phenological correspondence between fleshy-fruited plants and the abundance of frugivorous birds in temperate regions.

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Appendix 1. Frugivorous bird species observed from May 1995 to April 1997 at the study site.

White-bellied Green Pigeon (*Sphenurus sieboldii*)
 Japanese Green Woodpecker (*Picus awokera*)
 Great Spotted Woodpecker (*Dendrocopos major*)
 White-backed Woodpecker (*Dendrocopos leucotos*)
 Japanese Pygmy Woodpecker (*Dendrocopos kizuki*)
 Brown-eared Bulbul (*Hypsipetes amaurotis*)
 Red-flanked Bluetail (*Tarsiger cyanurus*)
 Daurian Redstart (*Phoenicurus aureus*)
 Scaly Thrush (*Zoothera dauma*)
 Japanese Thrush (*Turdus cardis*)
 Brown-headed Thrush (*Turdus chrysolaus*)
 Pale Thrush (*Turdus pallidus*)
 Eyebrowed Thrush (*Turdus obscurus*)
 Dusky Thrush (*Turdus naumanni*)
 Narcissus Flycatcher (*Ficedula narcissina*)
 Blue-and-white Flycatcher (*Cyanoptila cyanomelana*)
 Dark-sided Flycatcher (*Muscicapa sibirica*)
 Grey-streaked Flycatcher (*Muscicapa griseisticta*)
 Asian Brown Flycatcher (*Muscicapa dauurica*)
 Japanese White-eye (*Zosterops japonicus*)
 White-cheeked Starling (*Sturnus cineraceus*)
 Eurasian Jay (*Garrulus glandarius*)
 Carrion Crow (*Corvus corone*)
 Large-billed Crow (*Corvus macrorhynchos*)

Appendix 2. Flowering and fruiting periods of fleshy-fruited plants observed at the study site.

Species	1995–1996		1996–1997		Fruiting pattern
	Flowering period	Fruiting period	Flowering period	Fruiting period	
<i>Morus australis</i>	Apr.–May	Jun.–Aug.	May	Jun.–Jul.	S
<i>Broussonetia kazinoki</i>	May	Jun.–Aug.	May–Jun.	Jul.	S
<i>Prunus verecunda</i>	Apr.	Jun.	May	Jun.–Jul.	S
<i>P. jamasakura</i>	Apr.	Jun.–Jul.	Apr.–May	Jun.–Jul.	S
<i>P. apetala</i> ssp. <i>pilosa</i>	Apr.	May	Mar.–Apr.	May–Jul.	S
<i>P. grayana</i>	May	Jul.–Oct.	May	Aug.–Sep.	S
<i>Rubus crataegifolius</i>	May	Jun.–Jul.	May–Jun.	Jun.–Jul.	S
<i>R. microphyllus</i>	Apr.–May	Jun.–Jul.	May	Jun.–Jul.	S
<i>R. palmatus</i> var. <i>coptophyllus</i>	Apr.	May–Jul.	Apr.–May	Jun.–Jul.	S
<i>R. phoenicolasius</i>	Jun.	Jul.–Aug.	Jun.	Jul.	S
<i>R. parvifolius</i>	Jun.	Jul.	Jun.	Jul.	S
<i>R. hirsutus</i>	May	May–Jun.	May–Jun.	Jun.	S
<i>Coriaria japonica</i>	Apr.–May	Jun.–Jul.	May	Jul.	S
<i>Elaeagnus multiflora</i> var. <i>hortensis</i>	Apr.–May	Jun.	May	Jun.	S
<i>Swida controversa</i>	May	Jul.–Oct.	May–Jun.	Aug.	S
<i>Acanthopanax spinosus</i>	May	Jul.–Aug.	Jun.	Jul.–Aug.	S
<i>Sambucus racemosa</i> ssp. <i>sieboldiana</i>	Apr.	Jun.–Jul.	Apr.–May	Jun.–Jul.	S
<i>Viburnum plicatum</i> f. <i>glabrum</i>	May	Jul.–Aug.	May–Jun.	Jul.–Aug.	S
<i>Celtis sinensis</i> var. <i>japonica</i>	Apr.–May	Oct.–Jan.	May	Oct.–Dec.	F
<i>Magnolia salicifolia</i>	...	Sep.	F
<i>Neolitsea sericea</i>	...	Oct.–Feb.	Oct.	Oct.–Nov.	F
<i>Eurya japonica</i>	...	Oct.–Jan.	Apr.	Sep.–Dec.	F
<i>Sorbus commixta</i>	May	Oct.–Jan.	May	...	F
<i>S. alnifolia</i>	May	Oct.–Feb.	F
<i>Pourthiaea villosa</i>	May	Oct.–Feb.	May–Jun.	Nov.–Dec.	F
<i>Rosa multiflora</i>	May–Jun.	Oct.–Mar.	Jun.	Oct.–Jan.	F
<i>Mallotus japonicus</i>	Jun.–Jul.	Sep.–Jan.	Jul.	Sep.–Dec.	F
<i>Zanthoxylum piperitum</i>	May	Sep.–Nov.	May	Sep.–Nov.	F
<i>Z. schinifolium</i>	Aug.	Oct.–Jan.	Aug.	Oct.–Dec.	F
<i>Z. ailanthoides</i>	Jul.–Aug.	Oct.–Jan.	Aug.	Oct.–Dec.	F
<i>Rhus trichocarpa</i>	May	Aug.–Aug.	Jun.	Sep.–Dec.	F
<i>R. ambigua</i>	May	Aug.–Jul.	May–Jun.	...	F
<i>R. javanica</i> var. <i>roxburghii</i>	Aug.–Sep.	Oct.–Jul.	Aug.	Oct.–Feb.	F
<i>Meliosma myriantha</i>	Jun.	Oct.–Nov.	F
<i>Ilex macropoda</i>	...	Sep.–Dec.	F
<i>I. crenata</i> var. <i>paludosa</i>	Jun.	Oct.–Dec.	Jun.	Oct.	F
<i>Euonymus sieboldianus</i>	May–Jun.	Oct.–Nov.	Jun.	...	F
<i>E. alatus</i> f. <i>stiiatus</i>	May	Oct.–Jan.	May–Jun.	Oct.–Nov.	F
<i>E. oxyphyllus</i> var. <i>magnus</i>	Apr.–May	Aug.–Oct.	May–Jun.	Sep.	F
<i>Vitis flexuosa</i>	Jun.	Sep.–Dec.	Jun.	Sep.–Nov.	F
<i>Kalopanax pictus</i>	Jul.	Sep.–Oct.	F
<i>Aralia elata</i>	...	Oct.	Sep.	Oct.–Nov.	F
<i>Vaccinium oldhamii</i>	...	Sep.–Dec.	Jun.	Sep.–Dec.	F
<i>Ardisia japonica</i>	...	Oct.–Mar.	...	Oct.–Apr.	F
<i>Ligustrum tschonoskii</i>	Jun.	Oct.–May	Jun.–Jul.	Oct.–Jan.	F
<i>Clerodendrum trichotomum</i>	Aug.	Sep.–Nov.	Aug.	Sep.–Dec.	F
<i>Callicarpa japonica</i>	Jun.–Jul.	Sep.–Jan.	Jul.	Oct.–Dec.	F
<i>Lonicera japonica</i>	Jun.	Oct.–Feb.	Jun.	Oct.–Feb.	F
<i>Viburnum dilatatum</i>	May–Jun.	Sep.–Feb.	May–Jun.	Sep.–Jan.	F
<i>V. wrightii</i>	May	Sep.–Nov.	May	Sep.–Jan.	F
<i>Aucuba japonica</i> var. <i>borealis</i>	Apr.–May	Nov.–May	Mar.–May	Nov.–May	SP

S, F and SP represent the summer-, fall- and spring-fruited species, respectively.

Seed dispersal of Japanese stone pine by the Eurasian Nutcracker

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Abstract Seed dispersal of Japanese stone pine *Pinus pumila* by the Eurasian Nutcracker *Nucifraga caryocatactes* was studied at Mt. Apoi in Hokkaido, northern Japan. The seed foraging and caching behavior of diurnal birds and mammals was observed, and the relative importance of each species for pine seed dispersal was examined. All mature cones disappeared from the pine shrubs by mid-October each year regardless of the cone crop size. Eurasian Nutcrackers, Varied Tit *Parus varius*, Eurasian Nuthatch *Sitta europaea*, Red Squirrel *Sciurus vulgaris*, and Siberian Chipmunk *Tamias sibiricus* were all potential seed dispersal agents, however, observations revealed that nutcrackers carried 96% of all seeds transported from the pine trees. The nutcracker carried 142 seeds on average (max. 209) in one trip. Nutcrackers mainly carried pine seeds into their mixed coniferous forest, breeding habitat, where stone pines cannot normally become established and cached them in the soil there. Nutcracker caches averaged 12 seeds with a maximum of 51 seeds. Pine seedlings were found growing in clusters (in groups of two or more trees). The number of seedlings per cluster closely resembled the number of seeds in nutcracker caches. Results suggest that most stone pine seedlings originated from nutcracker caches. Eurasian Nutcrackers thus play an important role in the regeneration of Japanese stone pine despite their small number of caches.

Key words Caching behavior, *Nucifraga caryocatactes*, *Parus varius*, *Pinus pumila*, Scatter-board, *Sitta europaea*

Several members of the family Corvidae are known to store seeds and to be important seed dispersal agents (Turcek & Kelso 1968; Vander Wall & Balda 1981; Tomback & Linhart 1990; Vander Wall 1990). The interaction between Clark's Nutcracker *Nucifraga colombiana* and several pine species has been well studied in North America for *Pinus albicaulis* (Hutchins & Lanner 1982; Lanner 1982; Tomback 1982), *P. flexilis* (Lanner & Vander Wall 1980; Tomback & Kramer 1980), and *P. edulis* (Vander Wall & Balda 1977). Those studies documented the central role played by Clark's Nutcracker in the regeneration of the pines. Similar interactions were recognized between the Eurasian Nutcracker *N. caryocatactes* and *P. cembra* in Europe (Mattes 1982), *P. sibirica* in Siberia (Kondratov 1953; Reimers 1959), *P. koraiensis* in East Asia (Hutchins et al. 1996), and *P. pumila* (Saito 1983a; Hayashida 1994; Kajimoto et

al. 1998) and *P. parviflora* (Hayashida 1989a, 1994) in Japan.

Japanese stone pine *P. pumila* occurs from Siberia and Kamchatka south to Japan and Korea (Critchfield & Little 1966). A vegetation zone dominated by stone pine, known as the *P. pumila* zone, is present above the forest limit on most high mountains in northern Japan (Okitsu & Ito 1989; Yanagimachi & Ohmori 1991). The Japanese stone pine is a dwarf pine, and its thickets can regenerate vegetatively from adventitious roots (Okitsu & Ito 1984; Kajimoto 1992).

P. pumila has large wingless seeds, as do *P. albicaulis* and *P. cembra*, which belong to the Cembrae group within the genus *Pinus* (Mirov 1967). Several authors have reported that *P. pumila* seeds are cached by Eurasian Nutcrackers and germinate in their caches, as indicated by fragmentary observations of nutcracker behavior, cone and seed morphology, and seedling clumps (Saito 1983a; Hayashida 1994; Kajimoto et al. 1998). Previous studies of *P. pumila* dis-

persal have, however, lacked both quantified data of seed dispersal by animals and detailed behavioral observations of the animals dispersing the seeds.

The objective of the research described here was to determine the relative importance of the Eurasian Nutcracker and other potential dispersers for Japanese Stone Pine seed dispersal. The seed harvesting, transportation, and caching behavior of nutcrackers and other dispersal agents was studied in order to clarify the effects of animal behavior on pine seed regeneration.

STUDY AREA AND METHODS

1) Study area

The study was conducted on Mt. Apoi (811 m above sea level), which is located in south-central Hokkaido, Japan (42°06'N, 143°02'E). Mt. Apoi is composed of ultramafic rocks (dunite, lherzonite, etc.) of the Horoman peridotite complex (Niida 1984), and is covered with coniferous forests. The *P. pumila* zone extends from elevations of 500 to 800 m. Japanese white pine *Pinus parviflora* var. *pentaphylla* forest occupies the rocky slopes and ridges below 500 m, while the greater part of the mountain is covered by mixed coniferous stands dominated by *Picea glehnii*, *P. parviflora* var. *pentaphylla*, and *Abies sachalinensis* (Hayashida 1989a).

The soil (based on ultramafic rock peridotite) and meteorological conditions (frequent fog in summer and strong winds and little snow in winter), support a unique alpine flora despite the exceptionally low altitude (Tatewaki 1952). The height of the *P. pumila* scrub is dependent on the degree of wind exposure and snow depth (Okitsu & Ito 1984). Pine scrub (less than 100 cm tall) and alpine meadows predominate on wind-exposed ridges and slopes in the study area.

The native seed predators among birds are the Eurasian Nutcracker, Eurasian Jay *Garrulus glandarius*, Eurasian Nuthatch *Sitta europaea*, and several tits *Parus* spp. Nutcrackers can be observed in all seasons on Mt. Apoi, except in years when the Japanese stone pine and the Japanese white pine produce few cones. Although nesting by nutcrackers has not been confirmed in the area, there is no doubt that they do breed as they are often found in the mixed coniferous forest during the breeding season.

2) Cone fate and seed dispersal by vertebrates

Eight patches of *P. pumila* scrub (each patch had a 4 to 8 m² crown) were chosen for cone fate observa-

tion at elevations between 520 and 550 m. It takes two growing seasons for stone pine cones to mature. Immature second-year cones were mapped in each patch in June, and these cones were counted at intervals of two to four weeks until the cones were depleted. Data were collected from 1985 to 1990.

I gathered information on diurnal animal pine-seed harvesting rates, seed transportation, and seed caching behavior using 7× binoculars and a 25× telescope from an observation site at an elevation of 550 m. The observations were made within 900 m², including the eight patches for the cone fate studies. A total of 74.5 hours of observation were logged at the site from 21 August to 14 September 1985 (29.5 h), and from 12 August to 11 September 1987 (45 h). I usually observed from dawn till noon once or twice a week. Cone harvesting, cone transporting, feeding, seed harvesting, seed transporting, and seed caching were the recognized behaviors of various vertebrates. I recorded the frequency of seed transportation and the number of seeds carried each trip. These data were used to calculate the number of seeds transported per hour and to determine the relative number of seeds transported by each species.

Observations of seed storage behavior by birds and mammals at any time during the study periods were recorded. As nutcrackers flew to their caching sites after seed harvesting, it was difficult to follow them to observe caching behavior directly. Therefore I recorded the flight directions of the birds and the places where I lost sight of them, so as to be able to estimate where the caching sites were.

3) Seed caching by Eurasian Nutcrackers

Stored seeds are retrieved by nutcrackers and by other animals. Nutcrackers, however, probe into caches by thrusting their bills into the soil or forest litter, thus visible prod holes in the ground remain as signs of nutcrackers having dug up seed caches. Such excavations are easily distinguished from those of rodents. Rodent holes are three or more times larger than those made by nutcrackers, moreover, nutcrackers usually open the seeds at the recovery site, leaving behind a pile of seed coats (Tomback 1980), whereas rodents carry away seeds to consume them elsewhere. I followed such nutcracker holes on the ground and counted the number of seeds around or in caches along a 3.3 km long hiking trail (2.2 km in the mixed coniferous forest and 1.1 km in the *P. pumila* zone). This survey was conducted eight times in June and July 1986.

4) Clusters of Japanese stone pine trees

The seedlings of bird-dispersed pines have often been found in clusters consisting of several seedlings of the same age (Tomback 1982; Kajimoto et al. 1998). I counted *P. pumila* trees in two 5 m×5 m quadrats (Q1, Q2) and in a 10 m×10 m quadrat (Q3) in the *P. pumila* zone, in order to acquire information on the clumping frequency and age distribution of this species. Ages were determined by counting nodes and bud scars on trunks. I also recorded the numbers of seedlings and saplings on barren slopes along the hiking trail in the mixed coniferous forest (a 1.2 km line census, 5 m in width).

RESULTS

1) Cone fate

All second year cones of Japanese stone pine disappeared from the pine shrubs by mid-October every year, regardless of the size of the cone crop, and even though the crop size varied from year to year (Fig. 1). The cones began to disappear in early August in 1985, 1987, 1988, and 1990, and decreased rapidly from late August to mid-September. They had begun to disappear by mid-July in 1986 and 1989, and were depleted by late July. The pedicels of mature cones were loose enough to be detached easily from the branch, indicating that they might fall off under their own weight, however, I observed no intact cones falling to the ground beneath pine crowns. These findings indicate that the pine cones were harvested by animals.

2) Seed harvest and transportation by vertebrates

I observed twelve bird species and three mammal species in the study area during the study periods. These included the Eurasian Nutcracker, Eurasian Jay, Jungle Crow *Corvus macrorhynchos*, Oriental Greenfinch *Carduelis sinica*, Siberian Meadow Bunting *Emberiza cioides*, Eurasian Nuthatch *Sitta europaea*, Willow Tit *Parus montanus*, Coal Tit *P. ater*, Great Tit *P. major*, Varied Tit *P. varius*, Indian Tree Pipit *Anthus hodgsoni*, Great Spotted Woodpecker *Dendrocopos major*, Red Squirrel *Sciurus vulgaris*, Siberian Chipmunk *Tamias sibiricus*, and Snowshoe Hare *Lepus timidus*. Six species of these species (Eurasian Nutcracker, Oriental Greenfinch, Eurasian Nuthatch, Varied Tit, Red Squirrel, and Siberian Chipmunk) foraged on the pine seeds. The Oriental Greenfinch only ate pine seeds *in situ*, whereas the other five species harvested and trans-

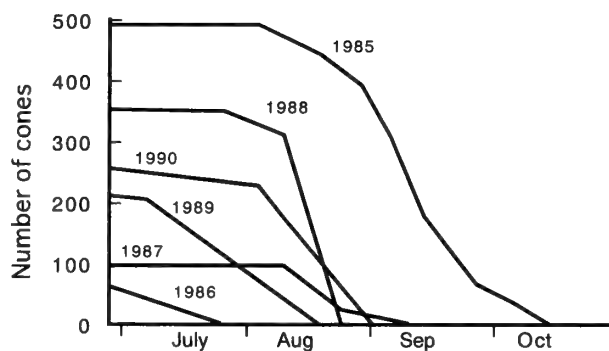


Fig. 1. Annual cone crop size and number of cones remaining on *Pinus pumila* trees 1985–1990. Data were collected from eight patches of *P. pumila* shrubs.

ported cones or seeds.

The nutcrackers began to forage on the stone pine cones as early as mid-July in 1986 and 1989, and in early August in 1985, 1987, 1988, and 1990. These foraging times coincided with the timing of cone disappearance (Fig. 1). During these periods, the cone scales were tight and the seed coats were thin and fragile. Consequently, nutcrackers and other animals were unable to pick up whole seeds and acquired only seed kernels directly from the cones. Some cones turned brown in mid-August and their seeds matured. Nutcrackers harvested the brown cones selectively and frequently transported the seeds. Nutcrackers were usually seen in pairs, and sometimes in small flocks of up to six birds.

Observations of nutcrackers foraging for cones followed a general pattern during which a bird first selected a cone then detached it by gripping it in the bill. Brown (mature) cones were easily detached from their subtending branches, and the detached cone was then carried in the bill to a perch on a rock, on the bough of a tall tree, or on the ground, where the bird extracted seeds from the cone. Following seed extraction, some seeds were squeezed in the bill until they cracked, then they were eaten. Most seeds derived from cones, however, were stored in the sublingual pouch rather than eaten. Each seed was apparently tested for edibility by rattling between the mandibles. Forty-three (95.6%) of the 45 pine seeds discarded by Nutcrackers were aborted (empty). Forty-two (32.3%) of the 130 seeds left behind on perches by nutcrackers after harvesting cones were aborted seeds. These facts demonstrate that Nutcrackers selectively transported only edible seeds.

Nutcrackers tip their heads upwards in an easily recognised motion, when pouching seeds for trans-

Table 1. Comparative transport of *Pinus pumila* seeds by five vertebrates during August and September in 1985 and 1987.

	Number of transporting per hour*	Number of seeds per transport**	Seeds transporting per hour	Relative number of seeds transported (seeds/10,000)
Nutcracker	2.07	142	293.94	9556
Varied Tit	1.54	1	1.54	50
Nuthatch	0.12	1	0.12	4
Squirrel	0.13	43	5.59	182
Chipmunk	0.16	40	6.40	208

* Total observation periods were 74.5 hours.

** Refer into text.

portation. Nutcrackers extracted 9–50 seeds (mean \pm SD = 29.2 ± 10.4 , $N=39$) from each cone, and required 15–78 seconds (mean \pm SD = 35.7 ± 22.5 , $N=7$) to do so. In each session, nutcrackers harvested 2–10 cones (mean \pm SD = 4.95 ± 1.88 , $N=20$). Therefore, nutcrackers carried 67–209 seeds (mean \pm SD = 142.2 ± 48.2 , $N=6$) in their sublingual pouches when flying to caching sites.

Varied Tits and Eurasian Nuthatches visited *P. pumila* shrubs in small mixed flocks or in pairs. They were unable to open the immature cones themselves and depended primarily on nutcrackers to expose the seeds for them. They were, however, able to extract seeds from more mature cones when seeds were slightly loose. When they successfully harvested a seed, Varied Tits and nuthatches flew 5–30 m to a tree in the coniferous forest. There they either ate or cached the seed and then returned to harvest another. Both Varied Tits and Eurasian Nuthatches transported seeds singly in the bill (Varied Tit $N=115$; Eurasian Nuthatch $N=9$). Both species usually stored seeds in tree branches or under bark, but occasionally cached seeds in the soil on the ground.

Red Squirrels were common inhabitants of the mixed coniferous forests on Mt. Apoi, and sometimes visited pine shrubs near the forest edges. Squirrels peeled off the cone scales to extract seeds, ate some seeds and then carried other intact cones in their mouths to the coniferous forest ($N=10$). As cones contained an average of 43 seeds (Hayashida 1994), Red Squirrels carried an average of 43 seeds each trip.

Siberian Chipmunks, as well as Red Squirrels, were found near the forest edges. Chipmunks harvested about 40 seeds at a time in their cheek pouches, and then returned to the forest ($N=12$). No data on Red Squirrel or chipmunk caching were ob-

tained during this study.

Of the five vertebrates observed transporting seeds Eurasian Nutcrackers and Varied Tits transported seeds most frequently (see Table 1). The relative number of seeds transported by each vertebrate, was calculated by multiplying the mean number of seeds per trip by the number of trips per hour. These calculations indicated that 96% of all the seeds transported, were carried by Eurasian Nutcrackers (Table 1).

3) Seed caching behavior by Eurasian Nutcrackers

Eurasian Nutcrackers transported seeds in all directions in both 1985 and 1987 (see Fig. 2). Most of the observed transport flights ranged from 100 to 1,000 m, with a few birds transporting seeds farther than 1,000 m. Transportation could be divided into two periods. In the first (mainly in August), they flew down into the mixed coniferous forest on all trips. During the second period (in September), the nutcrackers often carried seeds into the *P. pumila* zone (53% in 1985, 60% in 1987). Thus, 83% (79% in 1985, 86% in 1987) of seed transports by nutcrackers were into the mixed coniferous forests and 17% (21% in 1985, 14% in 1987) were into the *P. pumila* zone.

Nutcrackers stored *P. pumila* seeds in many different cache sites. I directly observed and confirmed nutcrackers making two caches consisting of two and twelve pine seeds in soil at depths of 1 to 2 cm. In addition caches ($N=26$) that I found near nutcracker excavations, the number of seeds per cache ranged from 1 to 51 (mean \pm SD = 12.0 ± 10.1). These caches were 1 to 3 cm deep in soil. Seven (27%) of the 26 caches were found in the *P. pumila* zone, and 19 (73%) in the mixed coniferous forest. The density of caches in *P. pumila* zone and the coniferous forest were 6.36 and 8.64 per km, respectively. These densi-

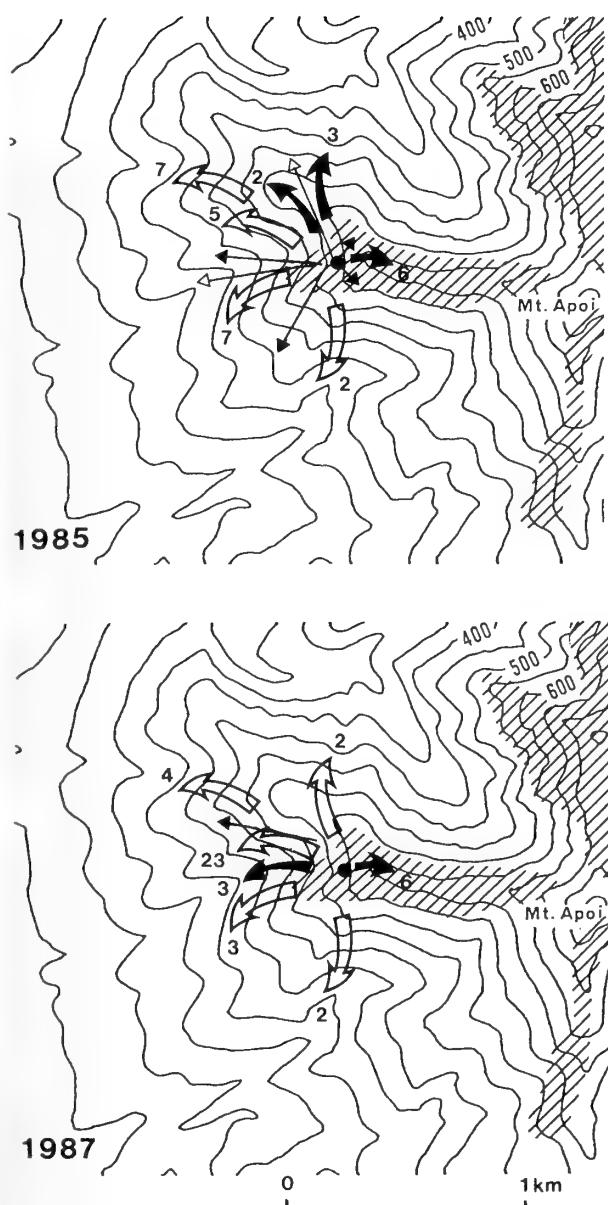


Fig. 2. The direction and frequency of seed transport by Nutcrackers in 1985 and 1987. Open arrows and solid arrows show the transporting directions in the first and second half of the observation periods, respectively. Figures show the frequency of transporting seeds in each direction. Small arrows indicate one trip in each direction. The hatched area is the *Pinus pumila* zone.

ties did not differ significantly ($\chi^2=0.5$, ns). One cache was found 2.8 km from the nearest seed source of *P. pumila*. Nutcracker not only predated seeds prior to germination, but also took emergent seeds (with a germinated but not expanded cotyledon). Nutcrackers predated 34% of the germinated seeds in 26 caches.

Table 2. Frequency of stem clustering in *Pinus pumila* in three quadrats and the line census.

	No. of cluster (%)		No. of individuals per cluster	
	single	≥ 2 trees	max.	mean \pm SD
Q1	29 (55)	24 (45)	16	2.5 ± 2.7
Q2	15 (34)	29 (66)	17	4.3 ± 3.8
Q3	19 (49)	20 (51)	5	1.8 ± 1.1
Line	9 (16)	47 (84)	26	5.6 ± 5.3

4) Clusters of Japanese stone pine trees

In the three quadrats studied in the *P. pumila* zone, the overall number of pine trees per cluster ranged from 1 to 17, and 53% of the clusters consisted of groups of two or more trees (Table 2). In the mixed coniferous forest, 84% of the 56 clusters of pine seedlings along the hiking trail were in groups of two or more trees. In particular, all seedlings under five years old were in groups of two or more trees. The mean number of individuals per cluster was 5.6, and the maximum number was 26 seedlings.

DISCUSSION

1) Seed dispersal agents of the Japanese stone pine

All Japanese stone pine cones in the Mt. Apo study area were carried away by animals by late autumn, even in years with bumper crops. Five species of vertebrates (Eurasian Nutcracker, Varied Tit, Eurasian Nuthatch, Red Squirrel, and Siberian Chipmunk) were found to be potential seed dispersal agents of the Japanese stone pine, and their contributions to seed dispersal were examined.

My observations indicated that the Eurasian Nutcracker is the most frequent harvester of pine cones. Nutcrackers in this study carried up to 209 pine seeds in their sublingual pouches, close to the maximum capacity of 218 seeds recorded in previous studies (Turcek & Kelso 1968). Mattes (1982) observed that Eurasian Nutcrackers carried up to 134 Cembra pine seeds, which were estimated to be 42.4 ml in capacity, based on comparison with the similarly sized Pinon pine seed (Vander Wall & Balda 1981). The volume of 209 Japanese stone pine seeds was measured using a graduated cylinder, and found to be 42.1 ml (Hayashida, unpublished data), consistent with the capacity reported by Mattes (1982).

The mean number of *P. pumila* seeds transported

by Eurasian Nutcrackers in their sublingual pouches was 142 in the Mt. Apoi study. Bergmann et al. (2001) reported that nutcrackers in the Russian Far East carried far fewer *P. pumila* seeds (80 on average) per trip, which represented the harvestable contents of 2.8 cones. In the Mt. Apoi study, however, the mean number of seeds counted is consistent with calculations of the number of seeds carried per trip (144.5), obtained by multiplying the average number of seeds extracted from each cone (29.2) by the average number of cones harvested per trip (4.95).

Varied Tits and Eurasian Nuthatches often harvested pine seeds and transported them singly to cache them under tree bark or in the ground. The Varied Tit has long been known to cache seeds (Higuchi 1977), storing as many as 63% of cached seeds of *Taxus cuspidata* on the ground (Sakakibara 1989), and thus playing an important role in forest regeneration. Nuthatches have also been observed to cache seeds (Hendricks 1995; Hutchins et al. 1996; Hardling et al. 1997). Based on their occasional ground caching behavior, both species may potentially help Japanese stone pine seedlings become established, however, as they only carry seeds one at a time their roles are probably not as important as that of the Eurasian Nutcracker.

Red Squirrels scatter-hoard Korean pine seeds in soil and contribute to the regeneration of Korean pine forest (Miyaki 1987; Hayashida 1989b). In contrast, they store whole cones of Japanese white pine (*P. parviflora* var. *pentaphylla*, the seeds of which are smaller than those of the Korean pine) in the ground (Hayashida 1988; 1989a). Although Red Squirrels were not observed caching cones during this study, they are suspected of storing whole Japanese stone pine cones because stone pine cones and seeds are similar in size to those of the white pine. An experiment by Saito (1983b) demonstrated that Japanese stone pine seeds in a cone buried in the soil are able to germinate, but are unable to become established as seedlings. These findings indicate that Red Squirrels do not play a role in the effective dispersal of the Japanese stone pine.

Siberian Chipmunks usually scatter and larder hoard acorns (Kawamichi 1980). They also harvest stone pine seeds and carry them in their cheek pouches. Hayashida (1989a) observed a chipmunk caching 33 Japanese white pine seeds in the ground at a depth of 3 cm, confirming that chipmunks can be seed dispersal agents. The frequency and quantity of seeds that they harvest are insignificant, however, in

comparison with the Eurasian Nutcracker.

In addition to the diurnal vertebrates, two nocturnal rodents are also potential seed dispersal agents in the study area. These are both wood mice *Apodemus speciosus* and *A. argenteus*, both of which scatter-hoard seeds (Imaizumi 1979; Miyaki & Kikuzawa 1988). Although these two mice are abundant in various forest types, they are uncommon in Japanese stone pine scrub (Ota 1968), thus nocturnal rodents are unlikely to be significant seed dispersers of *P. pumila*.

In northeast Siberia, the cones of *P. pumila* are a primary food source of Brown Bears *Ursus arctos* during the fall (Krechmar 1995). Although no Brown Bears were observed foraging in the Mt. Apoi study area, recent activity was evident. The large amount of fecal material left behind contained several thousand ingested cones but no intact seeds (Hayashida, unpublished data), suggesting that the brown bear is a seed predator and not a potential seed dispersal agent.

It is clear from various aspects of this study that the Eurasian Nutcracker transports most Japanese stone pine seeds, and that the Japanese stone pine depends mostly on nutcrackers for seed dispersal.

2) The behavior of the Eurasian Nutcracker as a seed dispersal agent of *P. pumila*

Eurasian Nutcrackers usually store more than one Japanese stone pine seed in a cache, as they do with the seeds of other stone pine species (Vander Wall & Balda 1977; Hutchins & Lanner 1982; Mattes 1982; Tomback 1982; Hutchins et al. 1996; Bergmann et al. 2001). Though they sometimes cache seeds under tree bark (Hayashida 1989a), most seeds are cached at depths of 1–3 cm in soil, in a microhabitat that is favorable for germination (Saito 1983b). The number of Japanese stone pine seeds in a single cache varied more widely than for other stone pines (Hutchins & Lanner, 1982; Tomback 1982; Hutchins et al. 1996), probably because the seed of *P. pumila* is smaller than that of other stone pine species.

Some experiments suggest that nutcrackers find most of their caches by memory (Balda 1980; Vander Wall 1982; Balda & Kamil 1989; Kamil et al. 1993; Kamil & Jones 1997), however, since germinated but not expanded cotyledon seeds were eaten along with ungerminated seeds from caches, nutcrackers may also find caches by using emergent seedlings as landmarks. If so, then many emergent pine seedlings may be damaged when birds dig up their caches. Though nutcrackers are principle predators of pine seeds, the

results of this study (cf. Table 2) and Kajimoto (2002) suggest that nutcrackers also play an important role in seed regeneration of *P. pumila*.

My observations indicated that nutcrackers transported most Japanese stone pine seeds to a mixed coniferous forest beyond the stone pine habitat. It is difficult for *P. pumila* seedlings to grow and become established on the dark floors of dense coniferous forests (Kajimoto 1995) even if cached seeds survive and germinate. Nutcrackers usually store seeds in the habitat of each pine species, as with most bird-dispersed pine species (Lanner & Vander Wall 1980; Hutchins & Lanner 1982; Mattes 1982; Tomback 1982), with the exceptions of *P. edulis* (Vander Wall & Balda 1977) and *P. monophylla* (Vander Wall 1988). Stands of these two pine species and those of Japanese stone pine do not provide suitable breeding habitat for nutcrackers, thus Eurasian Nutcrackers breed in coniferous forests (Yamashina 1934; Mattes 1982), and recover cached seeds to carry to their nestlings (Swanberg 1956). Transporting seeds into mixed coniferous forest (breeding habitat) allows for more efficient exploitation of the cached food during the breeding season.

Nutcrackers cached seeds in the coniferous forest in August and often cached seeds in the *P. pumila* zone in September. The reason for this shift in caching area is not clear, but it may be due to lower levels of cache robbing by rodents (e.g. squirrels, chipmunks, mice and voles) in the *P. pumila* zone than is likely to occur in the coniferous forests. Eurasian Nutcrackers disperse small amounts of Japanese stone pine seeds in the *P. pumila* zone, but their rate of seed retrieval is low and consequently seedlings become established especially during mast crop years.

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Relationship between seed retention time in bird's gut and fruit characteristics

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Abstract Seed retention time (SRT) of 16 fruit species in the guts of the Brown-eared Bulbul (*Hypsipetes amaurotis*), a major fruit consumer in central Japan, was studied to examine the relationship between SRT and fruit characteristics, i.e. fruit size, seed size, seed weight, and water content. Caged bulbuls were videotaped after feeding on fruits, and the time of defecation of each seed was recorded. Most seeds were always defecated in fecal pellets, with the exception of *Aucuba japonica* (the largest of the seeds studied), a seed of which was regurgitated on one occasion. Bulbuls defecate large seeds more rapidly than small seeds. The SRT of the last defecated seed, mean SRT, and standard deviation of SRT were significantly negatively correlated with seed size, fruit size, and seed weight, while SRT of the first defecated seed and water content were not correlated with any of the fruit characteristics examined. This suggests that Brown-eared Bulbuls are somehow able selectively to eliminate bulky seeds from the gut rapidly in order to overcome digestive limitations. If birds would prefer fruit species with large seeds that they can regurgitate and with short seed retention times in the gut, the results suggest that large seeds have the advantage of quantity of seed dispersed. Small seeds retained in the gut for longer have the advantage of being carried further and thus can achieve greater dispersal distances and more diverse destinations. The evolutionary interaction between fruiting plants and avian seed dispersers, may affect the diversity of fruit characteristics mediated by the length of retention time in a bird's gut.

Key words Frugivorous birds, Gut limitation, *Hypsipetes amaurotis*, Seed retention time, Seed size

Mutual interactions between birds and plants species have been emphasized in a range of studies of endozoochory, during which frugivorous birds consume fruit and subsequently disperse plant seeds (Snow 1971; Herrera 1985, 1995; Jordano 1995). There are, however, various conflicts between fruiting plants and frugivorous birds, for example, fruit pulp production is costly for plants, but provides frugivores with energy (Sorensen 1984; Fukui 1996). Fruiting plants and frugivorous birds are also in conflict over seed retention time (SRT), which is defined here as: the time from ingesting a fruit to the time when its seed(s) are eliminated, corresponding to the time spent passing through the bird's digestive system.

Several studies have suggested that seed dispersal distance is a function of SRT, however, small seeds tend to be dispersed further (Hoppes 1988; Murray et al. 1994), indicating a relationship between seed size and SRT. Small seeds tend to remain in the gut longer than large seeds. Furthermore, long SRT in the avian gut apparently enhances seed germination (Barnea et al. 1991). Seeds ingested by blackbirds *Turdus merula* usually had a higher germination rate than those ingested by bulbuls *Pycnonotus xanthopygos*. This differential rate in germination has been explained by longer SRT in blackbirds than in bulbuls. Longer SRT may increase abrasion of the seed coat by the avian digestive system and thus improve germination rate. SRT represents part of the handling cost of food for birds. Ingested seeds also represent a cost to frugivorous birds because the seeds displace gut volume that could otherwise be filled with digestible fruit pulp. Furthermore, the seed mass in-

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creases the energy demands for locomotion. Thus whereas long SRT is advantageous for fruiting plants, it is disadvantageous for frugivorous birds.

There are several ways to overcome gut limitations. One is enlargement of gut volume, as seen in large herbivorous mammals (Westby 1974). Gut volume enlargement is a less helpful solution for frugivorous birds as they must be highly mobile to visit ephemeral fruiting sources; increased gut volume brings the disadvantage of increased body weight and thus a severe restriction for actively flying birds. An alternative solution is more rapid food processing.

To reduce the ingestion cost of bulky seeds, frugivorous birds have several mechanisms for processing fruit quickly (Countney & Sallabanks 1992; Levey & Duke 1992). Levey (1987) identified two types of frugivorous birds in terms of their fruit processing mechanisms: mashers, and gulpers. Mashers include the tanagers Thraupidae and the finches Fringillidae, which crush fruits, separating the pulp from the seeds with their mandibles before ingesting only the pulp. Mashers solve the gut limitation problem by not ingesting seeds, but, as a result, their handling time costs are higher. Gulpers, including the manakins Pipridae, waxwings Bombycillidae, and thrushes Turdidae, ingest whole fruit, and separate the pulp from the seeds in their digestive system. Gulpers must offset their gut limitation by rapid elimination of seeds.

Gulpers ingest all seeds, regardless of seed size, then eliminate the seeds by either regurgitation or defecation (Levey 1987, 1992). Levey (1987) showed that seed size influenced processing methods and time. Frugivorous birds more frequently regurgitate large seeds (>4 mm) than small seeds (<2 mm). Median regurgitation times for two manakin species *Pipra mentalis* and *Manacus candei* were significantly less than that of defecation (Levey 1992). Regurgitated seeds only pass through part of a bird's digestive system, whereas defecated seeds pass through the whole process, and this may explain why regurgitation time is usually shorter than defecation time. Size is important in determining how quickly a seed can be voided with fecal matter (Levey 1992). Large seeds had a significantly shorter SRT in the Cedar Waxwing *Bombycilla cedrorum* than did small seeds. Rapid elimination of large bulky seeds may be one way for gulpers to overcome their gut limitations.

Understanding the relationship between seed size and seed retention time is essential when studying interactions between frugivorous birds and fruiting plants. Seed size is an important factor determining

the foraging efficiency of frugivorous birds. Seed size affects SRT, which is important for fruiting plants as it affects survival into the next generation. A number of studies have examined SRT in relation to seed size for various plant species (Sorensen 1984; Johnson et al. 1985; Levey 1987; Levey & Grajal 1991).

In this study, I examined fruit size and water content as well as seed size, since these characteristics appear to influence the foraging behaviour, digestion, and SRT of the Brown-eared Bulbul *Hypsipetes amaurotis*. The Brown-eared Bulbul is one of the major fruit consumers in central Japan, and an efficient seed disperser (Fukui 1995). When feeding, bulbuls usually gulp whole fruit, except when larger fruits are close in size to the gape width.

Sixteen fruit species with a wide range of fruit properties were used in feeding experiments with Brown-eared Bulbuls, and the relationship between fruit characteristics and SRT were analyzed statistically. The questions raised during this research, and discussed here are as follows: 1) Does the Brown-eared Bulbul regurgitate large seeds more frequently than small seeds?, 2) Does the bulbul eliminate large bulky seeds more rapidly than small seeds?, and 3) What properties of fruits affect seed retention time in the gut?

MATERIALS AND METHODS

1) Study area

This study was conducted on the University of Tsukuba campus, in southern Ibaraki Prefecture (36°06'N, 140°06'E), from 1989 to 1991. Six species of frugivorous birds were observed in the study area. These were the Brown-eared Bulbul, Gray Starling *Sturnus cineraceus*, Azure-winged Magpie *Cyanopica cyana*, Dusky Thrush *Turdus naumanni*, Pale Thrush *T. pallidus*, and Daurian Redstart *Phoenicurus aureus*. The Brown-eared Bulbul was the most abundant of the six, and the only one resident in the study area throughout the year.

2) Fruit characteristics

The Brown-eared Bulbul is a gulper known to feed on the fruits of 53 plant species from 24 families occurring in this study area (Fukui 1995). These fruits vary in diameter from 3.5 mm *Callicarpa mollis*, Verbenaceae to 12.0 mm *Aucuba japonica*, Cornaceae, and all were smaller than the maximum width of the bulbul's gape (17.0 ± 1.7 mm [mean \pm SE]). Sixteen common fruiting plants preferred by wild Brown-

Table 1. Characteristics of fruits examined.

Plant species	Seed size (mm)	Fruit size (mm)	Seed weight (mg)	Water content (%)
<i>Aucuba japonica</i>	16.1	16.5	0.69	74.36
<i>Daphniphyllum macropodum</i>	9.3	12.0	0.23	68.23
<i>Elaeagnus umbellata</i>	6.5	10.0	0.10	68.08
<i>Cinnamomum camphora</i>	6.3	8.5	0.12	56.29
<i>Paederia scandens</i>	6.2	6.2	0.029	65.68
<i>Ligustrum japonicum</i>	5.4	6.5	0.046	66.43
<i>Cornus florida</i>	5.3	11.0	0.091	64.9
<i>Nandina domestica</i>	5.1	6.5	0.10	66.98
<i>Viburnum dilatatum</i>	5.0	5.1	0.025	74.15
<i>Ilex crenata</i>	4.8	6.0	0.058	56.54
<i>Celastrus orbiculatus</i>	3.8	7.5	0.023	71.12
<i>Phytolacca americana</i>	3.0	8.0	0.0076	73.29
<i>Ilex serrata</i>	2.9	5.0	0.008	78.57
<i>Pyracantha angustifolia</i>	2.8	5.5	0.025	73.00
<i>Callicarpa mollis</i>	1.9	3.5	0.0031	79.35
<i>Eurya japonica</i>	1.8	6.0	0.0023	70.87

eared Bulbuls were chosen for this study (see Table 1). All 16 species produce fruit in autumn and winter. To minimize intraspecific variation in fruit features, I collected fruits for the experiments from a single mother tree within a five-day period.

For each of the 16 fruit species, four characteristics (Table 1) were recorded: fruit size, seed size, seed weight, and water content. Twenty or more fruits of each species were measured. Fruit and seed sizes, were the diameters of the longest axis measured using a pair of vernier callipers. Forty fresh fruits of each species were weighed individually with a Mettler balance. Seeds were removed from half of the 40 fruits and weighed. Another 20 fruits were dried in an oven at 60°C until their weights became constant. Water content was defined as the difference between dry weight and fresh fruit weight.

3) Seed retention times

Seven wild Brown-eared Bulbuls were captured with mist nets between September 1988 and March 1990. When captured they weighed 78.7 ± 9.6 g (mean \pm SE). These seven birds were housed indoors in separate cages (1.0 \times 1.0 m² \times 0.5 m high) and maintained on diets of wild fruits, pieces of apple, commercially-available food for fruit-eating birds, and water. All birds were fed commercially-available food overnight between the days of experiments and they were deprived of food for an hour prior to the onset of the experiments. Each bird was kept for a

week then released. All birds remained in good health throughout the duration of the experiments.

The SRT for the bulbuls was determined as follows. During experiments, each bulbul was fed on a single species of fruit and provided with plenty of water. From 1 to 20 fruits were supplied depending on fruit size (Table 1). Ten fruits of each of 16 plant species with intermediate sized fruits were given during experiments. There were three exceptions. Twenty fruits of *Callicarpa mollis* were supplied as this species bears very small fruit. Five fruits of the large fruit bearing *Daphniphyllum macropodum* were given, and just one fruit of the very large fruited *Aucuba japonica* was given. The number of experimental replications for each fruit ranged from 3 to 32, because the number of bulbuls available for testing varied from time to time.

Several experiments were carried out sequentially in a single day. One experiment consisted of supplying fruit followed by about two-hours of observation. Different fruit species were fed to a bird in successive experiments so as to be able to distinguish the seeds from each experiment. In each experiment the bulbuls consumed all the fruits within 20 seconds of them being provided. Each experiment was videotaped, and a sheet of graph paper on the floor of the cage made it possible to identify exactly the positions of feces, the condition of each fecal pellet, and the number of seeds in each fecal pellet. The time at which seeds were either defecated or regurgitated

was available in seconds from the video record. The SRT of each type of seed was calculated as the period between feeding and elimination.

Four indices were used to define the relationship between SRT and fruit characteristics: mean SRT, first SRT, last SRT, and standard deviation of SRT. Mean SRT was defined as the overall mean of the mean retention time for all defecated seeds in an experiment using a single fruit species. First SRT was defined as the overall mean SRT for the first defecated seed of each experiment. Last SRT was defined as the overall mean SRT for the last defecated seed of each experiment. The standard deviation of SRT was defined as the overall mean of the standard deviations of SRT for all defecated seeds in an experiment. The first three indices represent the SRTs of first, mean, and last defecated seeds of a given species, and thus they provide some indication of the expected dispersal distance and dispersal range of seeds by wild bulbuls. The standard deviation of SRT indicates the degree of variation in seed destination dispersal by birds, which, in addition to seed dispersal distance, is an important parameter of seed dispersal success for plants.

4) Analysis of seed retention time and fruit characteristics

Relationships between each index of seed retention time and fruit characteristics were analyzed using Pearson's correlation coefficient. All the data, except water content, were log-transformed before analysis. Water content data was transformed to arcsine square root in order to satisfy the requirement of normality.

RESULTS

1) Treatments of seeds

All but one of the seeds of all of the plant species used in the experiments were defecated by captive bulbuls. The exception was a single seed of *A. japonica*, which was regurgitated. The retention time of the regurgitated *A. japonica* seed was 14.2 minutes ($N=1$), but it was excluded from the calculation of retention time. All of the observed feces contained only seeds of a single species.

2) Individual difference between bulbuls

It was not practical to examine every fruit species with every bird, because the fruiting periods of the plants examined varied and each bulbul was retained for experimentation for just one week. One-way ANOVA was applied to the five fruit species for which SRTs were measured for two or three individual bulbuls. No significant differences were found among individual bulbuls in any of the experiments (Table 2).

3) Seed retention times

In most cases, seeds were defecated within one hour (Table 3). The mean SRT for all seed species was 20.8 minutes. The shortest SRT recorded was 2.4 for *Pyracantha angustifolia*, and the longest SRT recorded was 123.0 minutes for *C. mollis*.

4) Relationships between fruit characteristics and seed retention times

Last SRT and mean SRT were significantly negatively correlated with seed size, fruit size and seed weight (last SRT vs. seed size: $r=-0.68$, $N=16$, $p=0.0028$; mean SRT vs. seed size: $r=-0.56$,

Table 2. Comparison of retention time between individual birds.

Plant species	Individuals birds (# of seeds examined)	df	MS	F-ratio	P
<i>Ligustrum japonicum</i>	A vs B vs C (10, 10, 10)	2	317.63	.71	.50
<i>Pyracantha angustifolia</i>	A vs B vs C (80, 83, 91)	2	20.83	1.34	.26
<i>Ilex crenata</i>	C vs D vs E (20, 57, 51)	2	267.83	2.65	.07
<i>Aucuba japonica</i>	E vs F vs G (4, 13, 12)	2	6.15	.20	.82
<i>Cornus florida</i>	A vs B (46, 4)	1	4.91	.11	.74

Table 3. Seed Retention Times by Brown-eared Bulbul.

Plant name	N*	Mean of mean	Mean of first	Mean of last
<i>Aucuba japonica</i>	32	11.6±4.9	6.0	17.6
<i>Daphniphyllum macropodum</i>	17	15.7±5.5	9.5	30.0
<i>Elaeagnus umbellata</i>	4	19.8±7.2	7.0	31.8
<i>Cinnamomum camphora</i>	9	13.1±4.8	6.2	22.5
<i>Paederia scandens</i>	3	24.2±3.6	16.0	37.0
<i>Ligustrum japonicum</i>	4	12.1±7.4	3.0	26.5
<i>Cornus florida</i>	6	13.1±6.0	6.8	29.8
<i>Nandina domestica</i>	6	20.8±5.4	15.3	26.0
<i>Viburnum dilatatum</i>	4	28.0±15.5	11.6	59.1
<i>Ilex crenata</i>	4	21.5±12.0	2.5	53.6
<i>Celastrus orbiculatus</i>	4	26.9±10.6	14.5	42.5
<i>Phytolacca americana</i>	11	21.1±16.7	5.2	45.3
<i>Ilex serrata</i>	4	16.8±11.5	9.5	43.0
<i>Pyracantha angustifolia</i>	8	16.7±17.2	2.8	45.0
<i>Callicarpa mollis</i>	4	41.5±14.4	26.3	76.3
<i>Eurya japonica</i>	6	21.1±7.9	6.8	40.6

N* shows replications of trials of each fruit species.

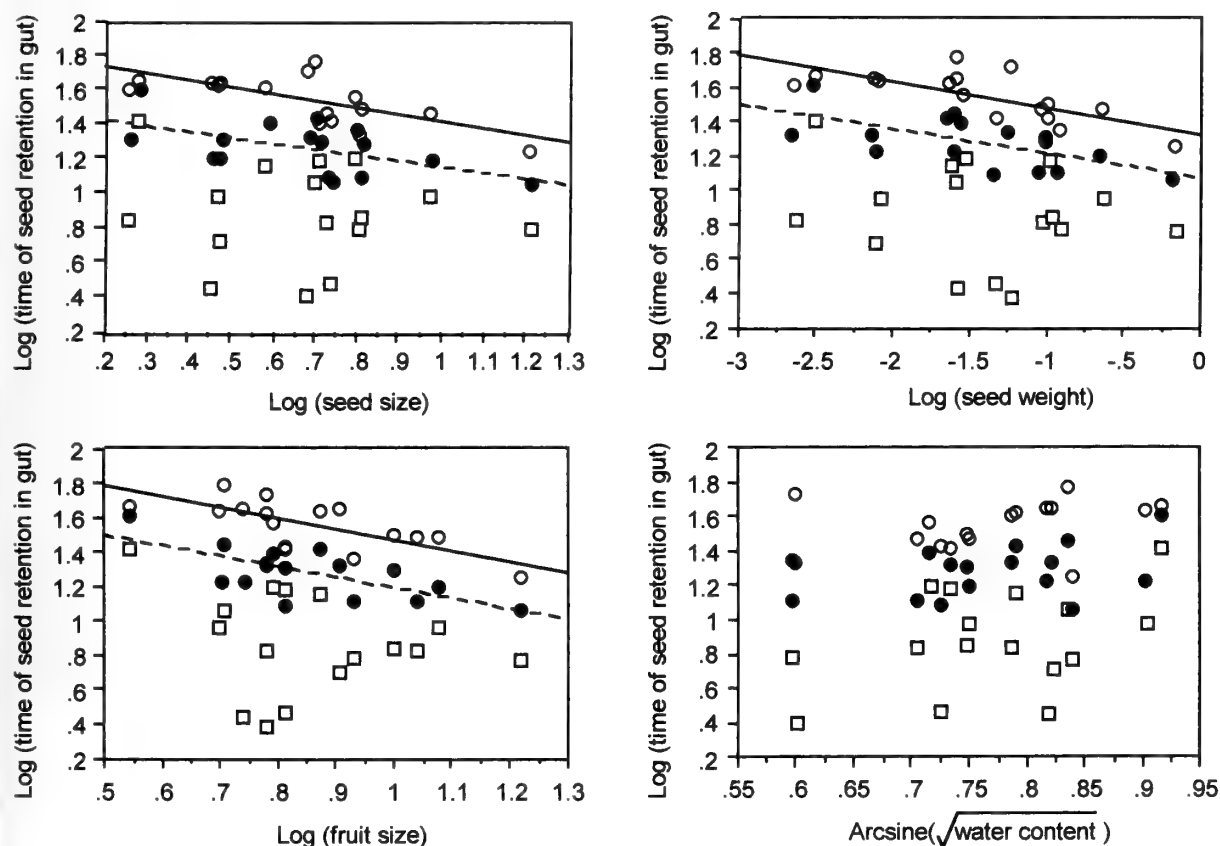


Fig. 1. Correlations between three indices of seed retention time (first SRT, mean SRT, and last SRT) and four fruit features (seed size, fruit size, seed weight and water content). Open squares=first SRT; solid circles=mean SRT, and open circles=last SRT. Unbroken lines indicate interactions between last SRT and each fruit feature. Broken lines indicate interactions between mean SRT and each fruit feature.

DISCUSSION

$N=16$, $p=0.022$; last SRT vs. fruit size: $r=-0.71$, $N=16$, $p=0.0014$; mean SRT vs. fruit size: $r=-0.68$, $N=16$, $p=0.0031$; last SRT vs. seed weight: $r=-0.71$, $N=16$, $p=0.0014$; mean SRT vs. seed weight: $r=-0.63$, $N=16$, $p=0.0077$) (see Table 1, Fig. 1). The first SRT did not have significant correlation with any fruit characters (seed size: $r=-0.12$, $N=16$, $p=0.66$; fruit size: $r=-0.24$, $N=16$, $p=0.38$; seed weight: $r=-0.23$, $N=16$, $p=0.41$). Water content was not significantly correlated with SRT (first SRT: $r=0.41$, $N=16$, $p=0.12$; mean SRT: $r=0.37$, $N=16$, $p=0.17$; last SRT: $r=0.28$, $N=16$, $p=0.30$).

The standard deviation of SRT was significantly negatively correlated with seed size ($r=-0.65$, $N=16$, $p=0.0053$), fruit size ($r=-0.57$, $N=16$, $p=0.021$), and seed weight ($r=-0.60$, $N=16$, $p=0.013$), but was not correlated with water content ($r=0.49$, $N=16$, $p=0.054$) (see Fig. 2).

As the key aspect of endozoochory is that plant seeds must pass through a bird's gut, seed retention time is a significant factor for both plants and birds. Brown-eared Bulbuls are gulpers, and so might be expected to overcome any gut limitation by rapid voiding of seeds, such as by regurgitation. During my experiments, a bulbul only once regurgitated a seed, and that was of *A. japonica*, which produces the largest seed of the fruits examined. Studies of manakins indicate that seed regurgitation is one way of voiding seeds rapidly in order to offset gut limitation because regurgitated seeds do not pass through the gut (Levey 1992). Levey (1992) found that manakins regurgitated large seeds more frequently than small seeds, whereas small seeds were always defecated. Like manakins, Brown-eared Bulbuls defecated small seeds and regurgitated a very large seed, although in the bulbul the average length of time to regurgitation

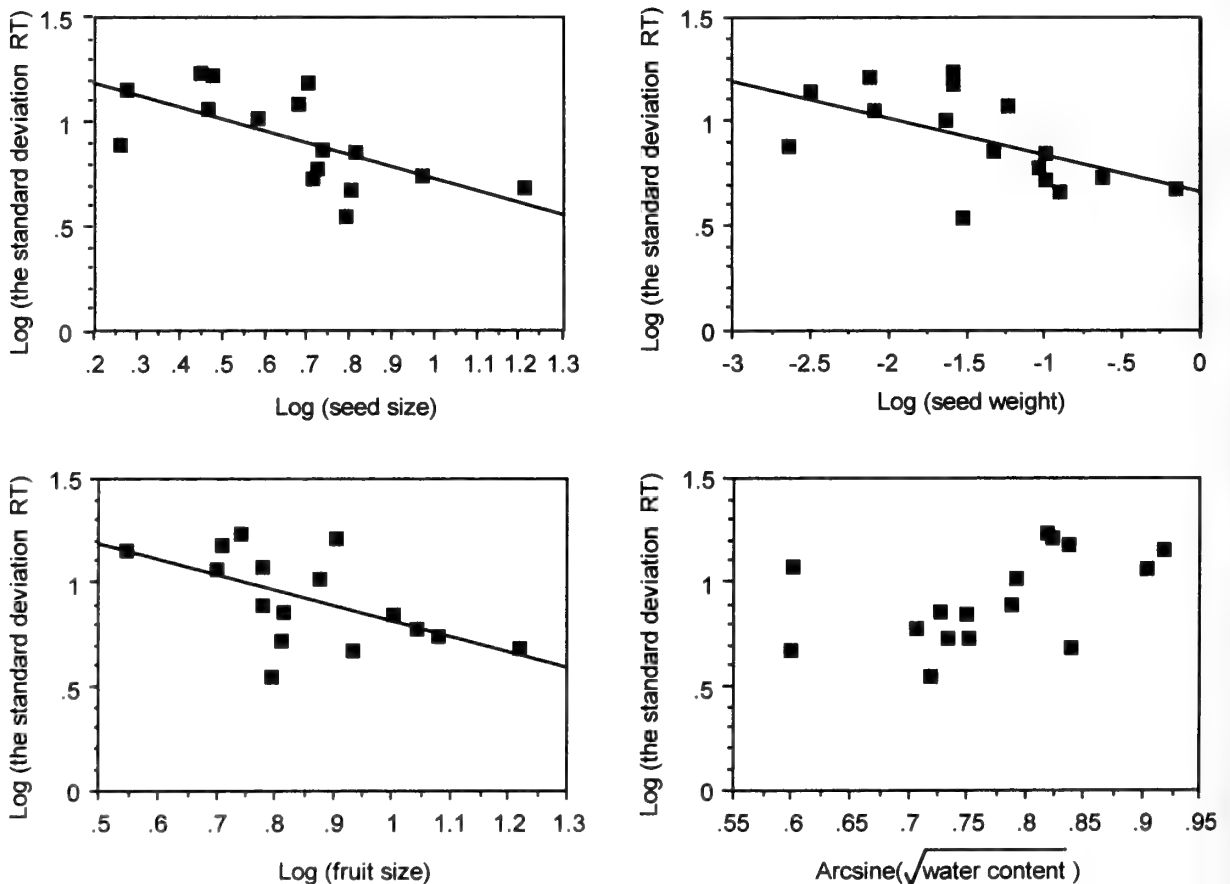


Fig. 2. The correlation between the standard deviation of SRT and four fruit features (seed size, fruit size, seed weight and water content). Unbroken lines indicate interactions between the standard deviation of SRT and each fruit feature (seed size, fruit size and seed weight).

is not known because regurgitation was observed only once.

The Brown-eared Bulbul defecated large bulky seeds more rapidly than small seeds (last SRT and mean SRT were both significantly negatively correlated with seed size, fruit size, and seed weight; see Fig. 1). These three fruit characteristics, representing bulk to frugivorous birds, being negatively correlated with SRT demonstrate that fruits and seeds with bulky characteristics are processed more quickly. In contrast, water content was not correlated with any indices of retention time, perhaps representing nutrient reward to frugivorous birds rather than bulk. It is concluded that it is important for bulbuls to process bulky seeds quickly. The first (shortest) SRT was not correlated with any of the four fruit characteristics examined (Fig. 1), indicating that gut limitations do not apply to first SRT.

For fruiting plants, rapid seed processing by birds is disadvantageous for their seed dispersal success. Since last SRT and mean SRT are considered to represent seed dispersal distances, the results imply that small seeds, which are retained in the gut longer, have longer dispersal distances than large seeds.

A large standard deviation of SRT is likely to correspond to high diversity of seed destination. If so, small seeds have a higher diversity of seed destination than large seeds because there was a negative correlation between seed size and the standard deviation of SRT (Fig. 2). The standard deviation of SRT was also negatively correlated with fruit size and seed weight. Thus, it is concluded that seeds within a small fruit or light seeds are dispersed at various destinations as well as at greater distances than larger, bulkier seeds.

Endozoochorous plants have evolved special features of their fruit to allow their dispersal agents to consume fruit easily (Gautier-Hion et al. 1985; Willson & Whelan 1990; Jordano 1995). Fruiting plants depending on frugivorous birds for their seed dispersal, are characterized by vivid colors (Willson & Whelan 1990). Among bird-dispersed fruits, nutritional characteristics differ between summer and winter fruit, coinciding with seasonal differences in the nutrient requirements of birds (Herrera 1982). Although such fruit characteristics are advantageous for frugivores, other characteristics, e.g. seed size, are disadvantageous (Sorensen 1984). Thus there exists a conflict between fruiting plants and frugivorous birds, although seed dispersal interactions have been discussed from the viewpoint of mutualism.

How quickly and how thoroughly seeds are processed has important evolutionary consequences for both fruiting plants and frugivores (Herrera 1995; Murray et al. 1994). Fruits are generally considered to be a food resource high in bulk (Herrera 1987), and bulk overloads the gut thereby reducing ingestion rate. Rapid seed processing may clear the gut and thus allow an increased ingestion rate (Levey & Grajal 1991; Levey 1992). Waxwings fed two types of artificial fruit (agar-based sugar solution as pulp and plastic beads as seeds) with equal seed loads but with different seed sizes consumed significantly more of the larger-seeded fruits. Because large seeds were defecated more quickly than small seeds, the increase in fruit consumption indicated that waxwings were process rate limited (Levey & Grajal 1991). Levey (1992) reported that freely feeding manakins took natural and artificial fruits very quickly after regurgitation. Evidence from various birds suggests that the seeds already in a bird's gut limit the rate of ingestion of more fruit. If rapid seed processing results in increased nutritional gain, then development of such an advantageous mechanism would spread through a population of frugivorous birds.

From the viewpoint of fruiting plants, seed dispersal success is determined by two factors: the quantity of seeds dispersed, and the distance over which seeds are dispersed. There is evidence that fruit species with seeds that are regurgitated, or with seeds that have short seed retention times (e.g. hawthorn *Crataegus monogyna*, sloe *Prunus spinosa*, and ivy *Hedera helix*) were the fruits most preferred by birds (Sorensen 1984). By implication, such fruit species have better chances of achieving higher removal rates of seeds, than other less-favored species. Considering that large seeds tend to have short retention times (Fig. 1), plant species producing large seeds benefit from the food preferences of birds and are able to disperse large numbers of their seeds, though their seed destinations may be limited because of the short throughput time. In contrast, plants producing small seeds (tending to have longer retention times) are more likely to achieve longer dispersal distances (corresponding to longer SRTs), which results in a greater diversity of seed destinations. Therefore, plants producing large seeds have the advantage of greater quantity of their seeds dispersed, whereas plants producing small seeds have the advantage of greater dispersal distances of their seeds.

The results from this study of the Brown-eared Bulbul imply that there are two types of fruit charac-

teristic associated with frugivorous birds in term of seed dispersal success. This evolutionary interaction between fruit plants and seed dispersers may affect the diversity of fruit features, e.g. seed size, fruit size and seed weight, mediated by the length of time the seeds are retained in a bird's gut.

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The role of the Velvet Asity *Philepitta castanea* in regeneration of understory shrubs in Madagascan rainforest

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Abstract In the Madagascan rainforest, the role of the Velvet Asity *Philepitta castanea*, an endemic frugivorous bird, in the regeneration of five understory shrub species (Myrsinaceae and Rubiaceae) was examined during the dry season (August to October). Effective dispersal distance was 33.3 m/h. Based on seed retention time in captivity, more than 85.7% of regurgitated seeds and all defecated seeds were estimated to be transported outside the crowns of mother plants. Seeds passed by the Velvet Asity germinated less successfully than unmanipulated (control) seeds in four out of the five species of shrubs. The reduced germination rate of processed seeds was partly due to the non-adapted morphology of the Velvet Asity as a seed disperser, in particular its voluminous, thick-walled, muscular gizzard. The narrow, slightly decurved bill and the semi-tubular tongue with vibrissae at the tip of this bird are normally features of insect- and/or nectar-eaters. Moreover, since manual removal of fruit pulp decreased the germination rate of seeds, the shrub species studied may not have developed adaptations for seed dispersal by animals. The most probable explanation for this situation is that the Velvet Asity has shifted relatively recently to occupy the niche of a fruit-eater of the understory and as yet insufficient time has passed for a sophisticated relationship with fruiting plants to have coevolved.

Key words Coevolution, Frugivory, Madagascar, Seed dispersal, Velvet Asity

In tropical forests, many trees bear fleshy fruits adapted for animal dispersal (Howe & Smallwood 1982; Janzen 1983), and the role played by animals, particularly by birds, is well documented (e.g., Howe 1977, 1981, 1986; Howe & Estabrook 1977; Murray 1988). That is, birds provide a survival advantage to fruiting plants by allowing them to escape seed predation near conspecific parent plants (Janzen 1970; Howe 1977; Regal 1977; Hubbel 1980; Gorchov et al. 1993). Most of the plants adapted to bird-dispersal have: red or black fruits to attract birds visually (Willson & Melampy 1983); relatively small fruits that are easily swallowed by birds (Wheelright 1985); and thin-husked fruit, which are quickly processed by birds (Leighton & Leighton 1983). Specialized fruit-

eating bird species involved in mutualistic interactions with such plants, typically have: a wide gape for swallowing large fruits whole (Snow & Snow 1988); a short intestine and a thin-walled, non-muscular gizzard for processing seeds gently and evacuating them quickly (Walsberg 1975); and a large liver for detoxifying fruits (Pulliainen et al. 1983).

The island of Madagascar, because of its ancient isolation from Africa, has a unique flora and fauna with a high proportion of endemic species, many of which are threatened by the rapid habitat destruction and forest fragmentation that has occurred in the last few decades and which continues today (Green & Sussman 1990; Ganzhorn et al. 1997). Understanding the relationships between frugivores and fruiting plants is extremely important for the preservation of these forest fragments because such interactions may influence plant distribution and floristic heterogeneity (Howe 1977). Belher and Böhning-Gaese (in press) have shown that frugivorous bird species are fewer,

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and their seed dispersal is far less efficient in Madagascar than in South Africa, while the seeds of Madagascan plants are less well adapted to bird-dispersal than those of South Africa.

The Velvet Asity *Philepitta castanea* is endemic to Madagascar where it is the only regularly fruit-eating bird species occurring among rainforest understory shrubs. This species consumes a wide variety of fruits throughout the year, and also feeds fruits to its young as an important dietary component during the breeding season (Rakotomanana & Hino 1998; Rakotomanana & René de Roland, in press). Nevertheless, this bird may not be fully adapted to frugivory as indicated by its narrow, slightly decurved-bill, a bill structure more typical of nectar- or insect-eaters (Langrand 1990; Yamagishi et al. 1997).

In this paper we describe research into the role of the Velvet Asity in the regeneration of five understory shrub species (*Oncostemon leprosum*, *Psychotria* sp. 1, sp. 6, sp. 8 and *Saldinia* sp.) in a southeastern Madagascan rainforest. We aimed to answer the following questions: (1) Whether the internal and external morphological characteristics of the Velvet Asity are adapted for seed dispersal, or not; (2) How far the birds disperse seeds by regurgitation and by defecation; (3) How successfully the seeds passed by the birds germinate and grow. Based on the results, we discuss the relationship that has coevolved between the Velvet Asity and the fruiting plants of Madagascar.

METHODS

1) Study area

The study was carried out in the Ranomafana tropical rainforest, about 365 km southeast of the capital Antananarivo, southeastern Madagascar (21°16'S–47°28'E), at an altitude of 800 to 1200 m above sea level. The study area was ca. 12.3 ha with many trails and paths. Two main seasons occur in the area: a rainy season (November–April) and a dry season (May–October). The annual precipitation was 2,600 mm (Nicoll & Langrand 1989) and the mean annual temperature was about 21.4°C (Ranomafana-Ifanadiana Station).

The vegetation was characterized by discontinuous canopy layers composed of scattered trees 20–30 m high. Trees over 30 m tall were rare in the forest, whereas the middle-canopy layer (4–10 m) was quite dense. Trees and shrubs consisted mainly of *Psychotria* spp. (Rubiaceae), *Oncostemon* spp. (Myrsi-

naceae), *Aphloia theaformis* (Flacourtiaceae), *Eugenia* spp. (Myrtaceae), *Ficus* spp. (Moraceae), *Dombeya* spp. (Sterculiaceae), *Tambourissa* spp. (Monimiaceae), *Ravensara* spp. (Lauraceae), *Polyscias* spp. (Araliaceae), and *Weinmannia* spp. (Cunoniaceae). Large areas of the forest floor are covered with an introduced exotic plant *Psidium cattleyanum*. The most common epiphyte was *Asplenium nidus* (Aspleniaceae) and the most common orchids were *Bulbophyllum* spp. and *Eulophiella* spp. (Orchidaceae).

2) Bird measurements

External morphometric measurements of Velvet Asity were obtained from museum specimens (Cornell University Museum, USA, the Peabody Museum, USA, and the Tsimbazaza Botanical and Zoological Park or PBZT, Madagascar) and from mist-net-captured birds in the field. Their bill, wing, tarsus and tail lengths were measured to the nearest 0.1 mm using callipers and birds were weighed to the nearest 0.1 g using a pesola balance. Captured birds were marked with colored plastic bands and released unharmed after being measured. The tongue and digestive tract of one individual (taken as a specimen for PBZT), were observed under a light microscope. Wing areas were also measured and wing loading was calculated as: body weight (g)/wing area (cm²), according to Pennycuik (1975) and Greenwalt (1975).

3) Field observations of foraging behavior

A total of 96 hours of field observations were made between 06:00 and 12:00 or between 14:00 and 17:00 from August to October in 1995 and 1996. Once a bird was found, we followed and recorded its foraging behavior until it was out of sight (using 10×40 binoculars and a tape recorder), using a continuous recording method (Martin & Bateson 1986). Both unmarked and marked birds (4 males and 11 females) were followed. One sequence of continuous recording averaged 69.8 min (range: 30–201 min, N=40 sequences). During each observation period, the times when birds visited and left each plant, and the foraging behavior of the focal bird, were recorded. The shrubs and trees that the birds visited were tagged with plastic tapes and marked on a map. For each movement, the distance in a straight line from the initial location where the bird was encountered was measured on this map. Median distances were calculated for every five-minute interval spent in move-

ment from the initial locations. A quadratic equation was devised to express the relationship between distance traveled and time elapsed during foraging movements.

4) Experimental determination of seed retention times

From August to October 1996, five Velvet Asity (2 males and 3 females) were mist-netted, and kept for experimental determination of seed retention time (SRT) of five common fruiting species: *O. leprosum*, *Psychotria* sp. 1, sp. 6, sp. 8 and *Saldinia* sp. (*Psychotria* species were identified by number, as their species names are not known; see Appendix 1). In the field, each captured individual was temporarily housed in a small cage (1 m×1 m×1 m) for a maximum of five hours, and supplied with ripe fruits of the target plant. One trial was conducted for each individual, and water was available during each trial. The number of fruits consumed was counted and the time from consumption to evacuation of seeds by regurgitation and defecation was measured using a stopwatch. Since uneaten fruits were removed five minutes after the first fruit was consumed, the number of ingested seeds differed among species (Appendix 2). Since we did not know exactly when the seeds evacuated were ingested, we used, as the time of ingestion, the midpoint of the interval during which fruits was consumed. Unclear data were removed from the analysis because determination of SRT is critical to the estimation of effective seed dispersal. After each trial, the bird was released unharmed. Processed seeds were classified as regurgitated (clean) and defecated (mixed with feces). Some SRT followed by regurgitation data were also obtained through direct observation in the field.

The distribution of the seeds dispersed (i.e. the seed shadow) by the Velvet Asity was estimated based on SRT followed by regurgitation or by defecation, for each shrub species, using the movement distance-time equation. Data relating to *Psychotria* sp. 1 and sp. 6, which have similar-sized seeds (Appendix 2), were combined owing to the small SRT sample sizes for each species.

5) Seed-germination experiment

Processed seeds (regurgitated and defecated by the Velvet Asity) and non-processed seeds (naturally-fallen fruits) of the five shrub species were collected from the forest floor and dried in a cool place over several weeks. Non-processed seeds were divided

into two groups; in one group (manipulated seeds) the pulp was manually removed, in the other group (control seeds) the pulp remained intact. Processed and non-processed seeds (excluding insect-damaged seeds) were used for germination experiments. Because all of the seeds of *O. leprosum* went rotten after defecation by the Velvet Asity, and because very few *Psychotria* sp. 8 seeds were defecated, defecated seeds could not be investigated in these two species.

Forty to two hundred seeds were used in germination experiments of each seed treatment of each shrub species. Seeds were planted in sand in small containers (28.5 cm length×24.5 cm width×5 cm height). The experiments were carried out in a glasshouse under constant luminosity and at a constant temperature of 24°C. Watering was twice a week. The germination of seeds, seedling survival, and seedling stem lengths, were all monitored at weekly intervals for 100 days after sowing.

RESULTS

1) Morphological characteristics

The average body weight and external morphometric measurements (accompanied with standard deviation and sample size in parentheses) of the adults were: body weight=8.9±3.2 g (19); bill length=18.1±1.9 mm (55), bill width=6.0±0.9 mm (55); bill depth=5.1±0.4 mm (55); tarsus length=24.3±2.4 mm (53); wing length=82.1±0.3 mm (55); tail length=42.5±0.5 mm (55). The bill was narrow (width/length=0.33±0.05 and depth/length=0.28±0.04), and slightly decurved.

The wing loading averaged 0.53 g/cm² (2), and the wing tip has poorly developed slots (Rakotomanana unpublished data). The tongue was semi-tubular with a deep cleft (5 mm in length) anteriorly with vibrissae at the tip (Fig. 1). The intestine was about 20 cm long and there was a muscular thick-walled (ca. 4 mm), voluminous gizzard (averaging 3% of body weight).

2) Foraging movements and behavior

Among foraging observations of the Velvet Asity 91.1% of items were ripe or partially-ripe fruits taken from understory shrubs (<7.5 m in height) belonging to the Rubiaceae and Myrsinaceae. The size and shape of fruits and the size and number of seeds varied among shrub species (Appendix 1). During field observations, birds were observed to take from 1 to 16 fruits from one shrub, depending on the size or abundance of fruits. The seeds were either regurgi-

tated or defecated away from the parent plants. The seeds of almost all of the larger fruits, such as *Psychotria* sp. 8, were regurgitated, not defecated.

The median distances of movement, measured in a straight line from the initial encounter point, increased almost linearly with increasing time and to 33.3 m in one hour (Fig. 2). The maximum distance was 58.4 m.

3) Seed retention time and seed-shadow

The Velvet Asity was observed to pluck fruit and

swallow them whole without manipulating them with its bill. All the seeds appeared to be voided intact through regurgitation and defecation. More than 60% of regurgitation of all five shrub species' seeds, was observed within 5–10 min after ingestion (Fig. 3). SRT data were obtained for *O. leprosum* in the field and experimentally, but there was no significant difference between them (χ^2 test=2.5, df=4, $P>0.05$). No seeds of *Psychotria* sp. 8 were observed to be defecated either in the field or in captivity (Appendix 2). SRT followed by defecation was more variable than SRT followed by regurgitation, with the exception of *Saldinia* sp. SRTs of the seeds of *Psychotria* sp. 1 and sp. 6 were longer than those of *O. leprosum* and *Saldinia* sp. (Fig. 4; Mann Whitney's *U* test, *Psychotria* sp. 1, sp. 6/*O. leprosum*, $z=-4.7$, $P<0.001$, *Psychotria* sp. 1, sp. 6/*Saldinia* sp., $z=-5.7$, $P<0.001$ and *O. leprosum*/*Saldinia* sp., $z=-1.7$, NS).

The estimated maximum distances of dispersal by regurgitation were 18.2 m in *O. leprosum*, 5.4 m in *Saldinia* sp, 6.7 m in *Psychotria* sp. 1, 18.7 m in *Psychotria* sp. 6, and 13.8 m in *Psychotria* sp. 8 (Fig. 5). Defecated seeds were transported farther than regurgitated seeds (Fig. 4). The dispersal distances by defecation were estimated to range from 8.5 m to 18.7 m in *O. leprosum*, from 9.1 m to 15.4 m in *Saldinia* sp, and from 14.4 m to 29.0 m in *Psychotria* sp. 1 and sp. 6. The average crown diameters of the understory shrubs were 1.6 ± 0.8 m in *O. leprosum*, $1.9\text{ m}\pm0.6$ m in *Psychotria* sp. 1, 1.6 ± 0.5 m in *Psychotria* sp. 6, 2.8 ± 0.9 m in *Psychotria* sp. 8, and

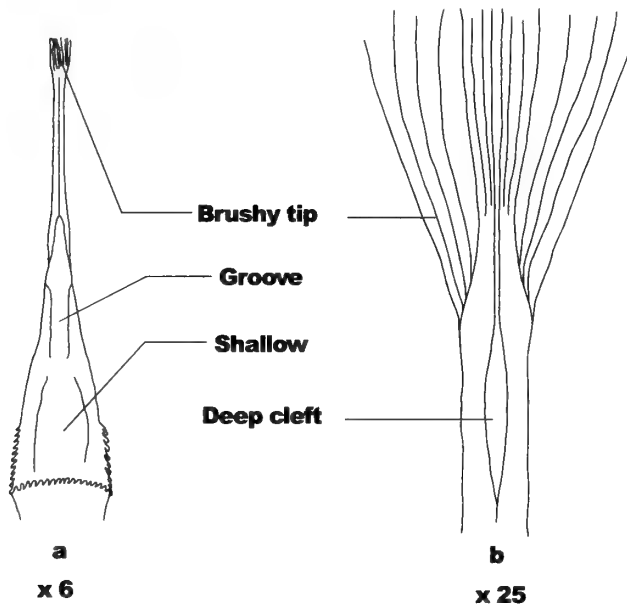


Fig. 1. (a) The whole tongue and (b) tongue tip of *P. castanea*.

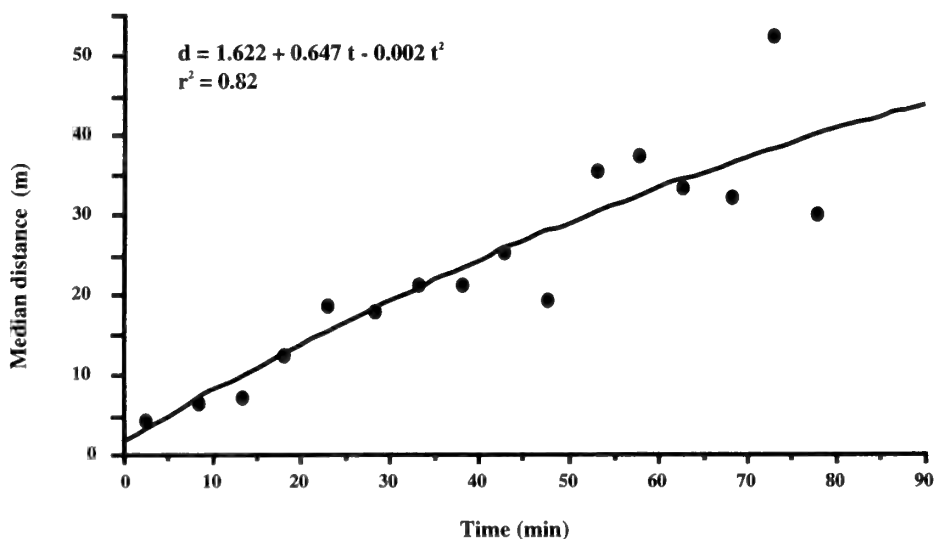


Fig. 2. Relationship between time and median distance of movement in a straight line from the initial encounter point.

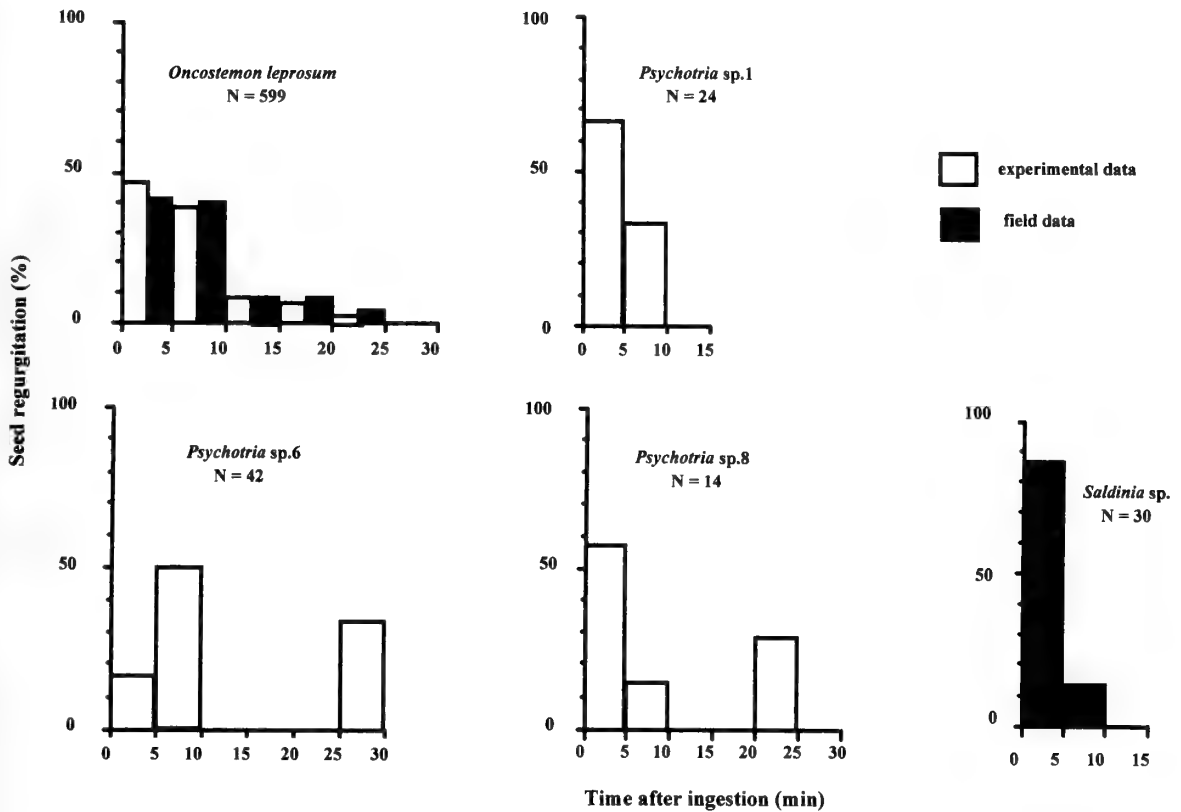


Fig. 3. SRT of seeds regurgitated by *P. castanea* for each of five shrub species.

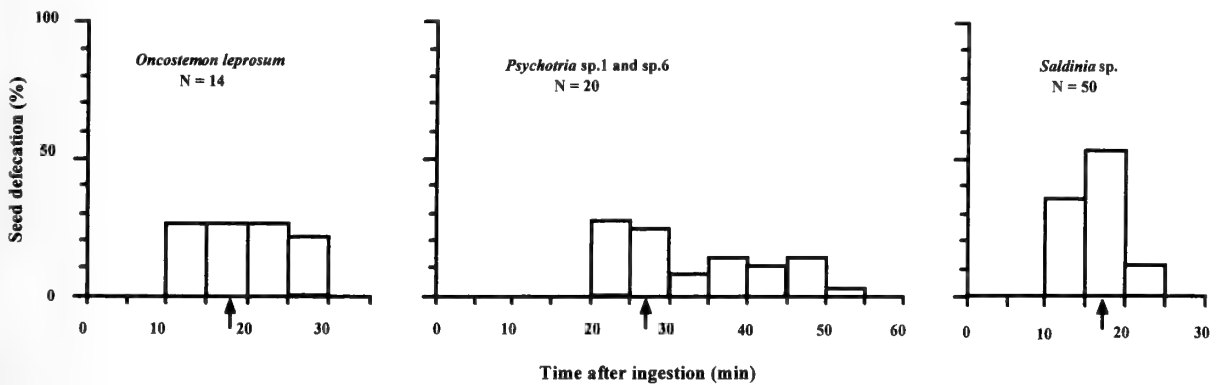


Fig. 4. SRT of seeds defecated by *P. castanea* for each of five shrub species. Arrows correspond to median passage times.

1.7±0.6 m in *Saldinia sp.* (N=20 for each species). Thus for all of the five shrub species more than 85.7% of the regurgitated seeds and all of the defecated seeds were estimated to be transported beyond the crown of the mother plant.

4) Germination ratios and growth rates of processed and non-processed seeds

Seed-germination experiments revealed that the

Velvet Asity has a negative effect on the germination of the seeds of four of the five shrub species (*Psychotria sp. 8* was the exception) (Table 1). The processed and manipulated seeds of *Saldinia sp.*, *Psychotria sp. 1* and *Psychotria sp. 6* germinated less successfully than their control seeds. The processed seeds of *O. leprosum* all went rotten before germination, although the germination ratio of manipulated seeds was higher than the control seeds. No differences in ger-

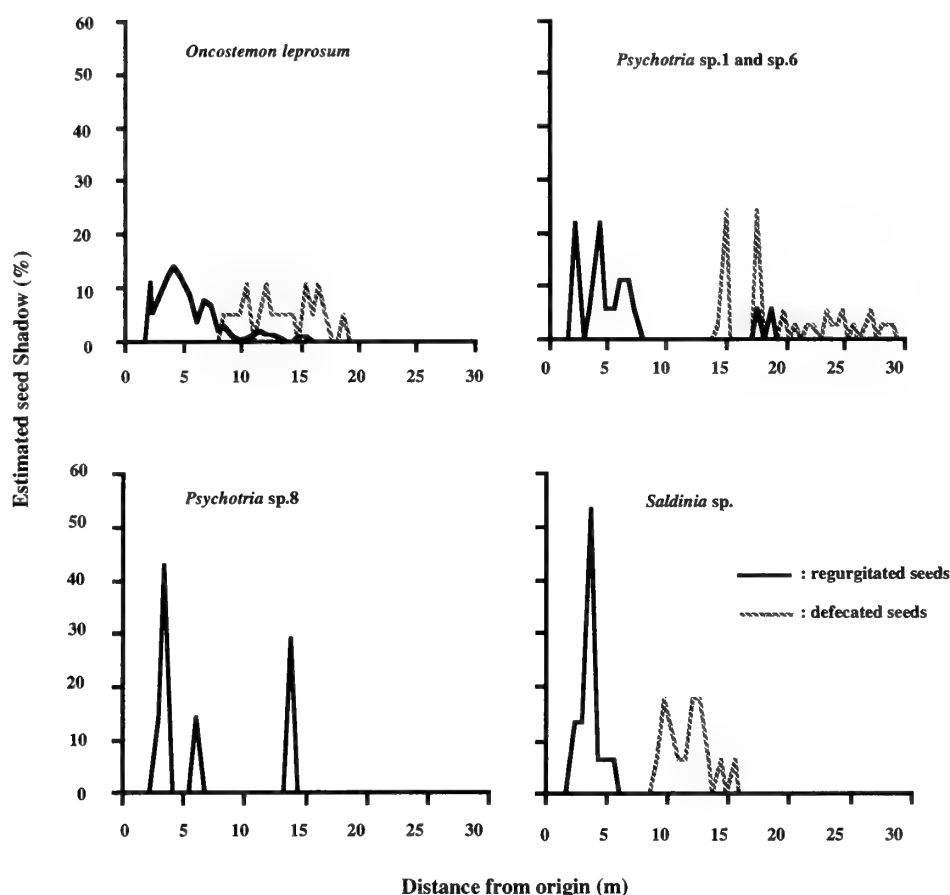


Fig. 5. Estimated seed shadow produced by regurgitation and defecation for each of five shrub species.

Table 1. Cumulative germination ratios (%) of seeds at 100 days in four treatments for five shrub species. Sample sizes are shown in parentheses. The same letters indicate significant differences between treatments for each species, with Fisher's exact test (Bonferroni's method, $P < 0.05$).

	<i>Oncostemon leprosum</i>	<i>Psychotria</i> sp. 1	<i>Psychotria</i> sp. 6	<i>Psychotria</i> sp. 8	<i>Saldinia</i> sp.
Control	11.7 (60) ^a	37.5 (200) ^{abc}	55.0 (200) ^{abc}	14.5 (200) ^{ab}	66.5 (200) ^{abc}
Manipulated	35.0 (60) ^{ab}	17.0 (100) ^{ad}	25.0 (100) ^a	39.0 (100) ^a	30.5 (200) ^a
Regurgitated	0.0 (24) ^b	6.0 (200) ^{bd}	11.0 (50) ^b	39.0 (100) ^b	40.0 (80) ^b
Defecated	—	7.0 (100) ^c	8.0 (50) ^c	—	32.0 (50) ^c
χ^2	17.4	77.5	148.7	65.9	58.3
d.f.	2	3	3	2	3
P	<.001	<.0001	<.0001	<.0001	<.0001

—: Not investigated.

mination rates were found between regurgitated and defecated seeds in four species. For *Psychotria* sp. 8, however, regurgitated and manipulated seeds germinated more successfully than the control seeds.

On the other hand, the Velvet Asity had a positive effect on the growth rates of seedlings after germination. In *Psychotria* sp. 1 and sp. 6 and *Saldinia* sp.,

the seedlings that germinated from defecated seeds were significantly taller than, or not different from, those from other treatments, although those from regurgitated seeds were shorter than their control seeds. In *O. leprosum* and *Psychotria* sp. 8, for which defecated seeds were not investigated, the seedlings that germinated from manipulated or regurgitated seeds

Table 2. Stem lengths (mean \pm SD) of seedlings at 100 days after sowing in four treatments for five shrub species. Sample sizes are shown in parentheses. The same letters indicate significant differences between treatments for each species, with post-hoc F-test (Bonferroni's method, $P < 0.05$).

	<i>Oncostemon leprosum</i>	<i>Psychotria</i> sp. 1	<i>Psychotria</i> sp. 6	<i>Psychotria</i> sp. 8	<i>Saladinia</i> sp.
Control	20.0 \pm 1.2 (7) ^a	29.0 \pm 0.7 (70) ^{abc}	25.0 \pm 0.8 (105) ^{ab}	15.0 \pm 0.8 (26) ^{ab}	31.0 \pm 1.1 (130) ^{abc}
Manipulated	30.0 \pm 0.9 (14) ^a	23.0 \pm 0.6 (12) ^{ade}	26.0 \pm 1.0 (12) ^{ac}	35.0 \pm 0.8 (39) ^{ac}	27.0 \pm 0.8 (51) ^{ade}
Regurgitated	—	24.0 \pm 0.7 (12) ^{bdf}	21.0 \pm 1.3 (6) ^{bcd}	40.0 \pm 1.1 (33) ^{bc}	28.0 \pm 0.8 (30) ^{bdf}
Defecated	—	30.0 \pm 0.8 (7) ^{cef}	25.0 \pm 0.8 (4) ^d	—	35.0 \pm 0.8 (14) ^{cef}
F	492.6	358.6	5746.1	357.6	357.6
d.f.	1	3	3	2	3
	$P < .0001$	$< .0001$	$< .0001$	$< .0001$	$< .0001$

—: Not investigated.

were significantly taller than those from the control seeds (Table 2).

DISCUSSION

The seed shadow produced by the Velvet Asity indicates some contribution of this bird to the seed dispersal of shrubs in the Madagascan rainforest, although the maximum dispersal distance (58.4 m) was much shorter than that of Neotropical frugivorous birds (ca. 220–510 m, Murray 1988). The short dispersal distances recorded in Madagascar might be due to the Velvet Asity's aerodynamically non-advanced wing features, such as its short wings, high wing loading, and poorly slotted wing, which would produce poor lift and acceleration during flight (Savile 1957; Pennycuik 1969, 1975; Norberg 1981; Rayner 1981; Rakotomanana 1998).

The Velvet Asity has some of the general features of specialized fruit-eaters, including, for example, a diet consisting mostly of fruits (Snow 1980; Morton 1973), great attentiveness and faithfulness to fruiting plants, the habit of regurgitating seeds, rapid passage of seeds through the gut (McKey 1975), and possession of a short digestive tract (Desselberger 1931; Docters Van Leeuwen 1954; Walsberg 1975). The decreased germination ratios of seeds regurgitated or defecated by the Velvet Asity demonstrate, however, that this species may not be adapted for dispersing seeds of fruiting plants. The rough chemical and physical treatment experienced inside the bird's muscular, thick-walled, voluminous gizzard, which is twice the size of that of a specialized frugivorous bird such as *Phainopepla nitens* (Walsberg 1975), may cause seed damage, indicating that the Velvet Asity is

partially a seed predator. Although the Velvet Asity's narrow, slightly decurved bill, and its semi-tubular tongue with vibrissae at the tip, may help it obtain insects (Gardner 1925) and/or nectar, these characteristics are unlikely to be useful for seed-eating (Amadon 1950; Richard & Bock 1973).

Only *Psychotria* sp. 8 which produces seeds with a thick, hard seed coat, benefited from processing in the Velvet Asity's gut, and from artificial manipulation. This species of shrub may have adapted to seed dispersal by the Velvet Asity, although its foraging preference was not high when compared with other species owing to the large size of its fruits (Rakotomanana & Hino 1998). Since the control seeds, with pulp, germinated more successfully than manipulated seeds, without pulp, however, the shrub species other than *Psychotria* sp. 8 may not have developed adaptations for seed dispersal by animals including birds.

How do we explain the current relationship between the Velvet Asity and the understory shrub species, in which the asity appears to be a partial seed predator, but one that carries seeds some distance from the mother plant? The most probable explanation is that the Velvet Asity has shifted relatively recently from being an insect- and/or nectar-eater to being a frugivore in the understory and as yet insufficient time has passed for a sophisticated relationship with fruiting plants to have coevolved. That a niche shift may have occurred, is indicated by the morphological structure of the Velvet Asity's bill and tongue, and by observations that show that it takes arthropods and nectar on rare occasions (Prum & Razafindratsita 1997; Rakotomanana et al. in press). In addition, two species of Sunbird-Asity *Neodrepanis coruscans* and

N. hypoxantha, which are classified in the same endemic family, Philepittidae, as the Velvet Asity, and considered to have the same ancestral origins as the Velvet Asity, both feed mainly on nectar and insects and have long, thin, decurved bills (Langrand 1990; Morris & Hawkins 1998) and tubular tongues (Morioka, unpublished).

In Madagascar, lemurs are also important seed-dispersers. In the same forest in which our study site was located, Dew and Wright (1998) have shown that seeds passed by lemurs germinate more successfully, and grow faster than those not passed by lemurs, indicating mutualistic adaptations between lemurs and fruiting plants. Dew and Wright (1998) also suggested that fruits more than 10 mm in diameter are most likely to be dispersed by lemurs, while those less than 10 mm in diameter are most likely to be dispersed by birds. The fruits of four of the five shrub species we studied were less than 10 mm in diameter, only *Psychotria* sp. 8 fruits were larger. Evidently, based on fruit size, seed dispersal of these fruiting plants should depend primarily on birds. If they are indeed dependent on the Velvet Asity for seed dispersal, how have these fruiting plants maintained their populations in spite of their low germination success rate? In order to understand the dynamics of understory shrub survival it is necessary to examine plant seed dispersal in more detail, examining not only the contribution of the Velvet Asity, but also that of occasional frugivorous visitors such as the Madagascar Bulbul *Hypsipetes madagascariensis*, the Red-fronted Brown Lemur *Eulemur fulvus rufus* and the Red-bellied Lemur *Eulemur rubriventer*, and bats such as *Pteropus rufus* and *Rousettus madagascariensis*.

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Appendix 1. Fruit characteristics of five shrub species.

	<i>Oncostemon leprosum</i>	<i>Psychotria</i> sp. 1	<i>Psychotria</i> sp. 6	<i>Psychotria</i> sp. 8	<i>Saldinia</i> sp.
Plant family	Myrsinaceae	Rubiaceae	Rubiaceae	Rubiaceae	Rubiaceae
Fruit colour	red	red	blue	red	blue
Fruit type	berry	berry	berry	berry	berry
Fruit shape	round	ovoid	ovoid	ovoid	round
Seeds number	1	1 or 2	1 or 2	1 or 2	1 or 2
Average fruit size (mm) ^a	7.1	5.9	7.3	11.9	8.2
Average seed size (mm) ^b	4.9	4.7	4.8	9.6	2.8

a: Number of sample is 60 for each species.

b: Samples were 122, 30, 84, 42 and 185 in the order of species from the left.

Appendix 2. The number of fruits ingested and seeds processed by the Velvet Asity for each shrub species in the cage experiment.

	<i>Oncostemon leprosum</i>	<i>Psychotria</i> sp. 1	<i>Psychotria</i> sp. 6	<i>Psychotria</i> sp. 8	<i>Saldinia</i> sp.
Ingested fruits	139	35	50	7	52
Regurgitated seeds	125	24	42	14	2
Defecated seeds	14	18	2	0	50

ORIGINAL ARTICLE

Head-bobbing patterns, while walking, of Black-winged Stilts *Himantopus himantopus* and various herons

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ORNITHOLOGICAL SCIENCE

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Abstract Head bobbing patterns of walking Black-winged Stilts *Himantopus himantopus* and eight species of herons were studied. Though several of the species studied had been previously reported as non-bobbing birds, all nine species usually head bobbed while walking during our observations. The head-bobbing pattern most frequently observed was 'one bob per step' in which a bird bobs its head once for each step it takes. In several species, one of two other patterns was also observed. The 'one bob per two steps' pattern was observed in three species of herons when they were walking slowly, and the 'two bobs per step' pattern was observed in Black-winged Stilts. Non-bobbing walking was observed in Japanese Night Herons *Gorsachius gossaga* walking at relatively fast speed during foraging, and in two other species of herons when they were not foraging. Head bobbing may be affected by walking speed and by whether birds are foraging or not.

Key words Black-winged Stilts, Foraging, Head-bobbing patterns, Herons, Non-bobbing walking

Many birds head bob while walking, and most bob once for each step (Daanje 1951; Bangert 1969). During head bobbing, the head is held stable relative to the environment during the hold phase and is thrust forward during the thrust phase (Dunlap & Mowrer 1930; Whiteside 1967). Previous studies have provided evidence that head bobbing has visual functions (Friedman 1975; Frost 1978; Pratt 1982; Davies and Green 1988; Wallman & Letelier 1993; Green et al. 1998; Troje & Frost 2000). In addition, a neural constraint (Troje & Frost 2000) and a biomechanical function (Fujita 2002) have been proposed as the factors facilitating synchronization of head and leg movements of walking birds.

Nevertheless, it is not clear why some birds bob their head during walking while others walk without doing it. Dagg (1977), the only author to have made an issue of this question, listed 28 head-bobbing and

21 non-bobbing species and mentioned that most non-bobbers generally live near water, whereas head-bobbers generally eat seeds or fruits rather than moving prey. Dagg's (1977) results were based, however, on small numbers of walking steps, and no other information (such as walking speed, ground condition, walking situation) was given. Since several species walk both with and without head bobbing (Dagg 1977), detailed observations are required before a species can be confirmed exactly as only a head-bobber or a non-bobber.

The present study provides more detailed information on several species classified as non-bobbers by Dagg (1977) and on several related species. These were the Japanese Night Heron *Gorsachius gossaga*, Malayan Night Heron *G. melanolophus*, Cattle Egret *Bubulcus ibis*, Intermediate Egret *Egretta intermedia*, Little Egret *E. garzetta*, Pacific Reef Egret *E. sacra*, Gray Heron *Ardea cinerea*, Purple Heron *A. purpurea*, and Black-winged Stilt *Himantopus himantopus*. Observation of these species was expected to provide insight into the common characteristics of head-bobbers because all nine species live near water

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and eat small animal prey.

MATERIALS AND METHODS

The walking behavior of wild individuals of nine species (eight herons/egrets and one shorebird) was filmed using a DCR-TRV30 digital video camera (SONY, Tokyo, Japan).

Video films were analyzed first to show whether birds walked with or without head bobbing. Head-bobbing while walking was defined as walking while alternately extending and flexing the neck, and non-bobbing walking was defined as walking without obvious neck extension or flexion. When birds were walking away from, or towards, the camera, it was difficult to distinguish whether head bobbing occurred or not, thus those observations were discarded.

Subsequent analysis focussed on the number of bobs per step among head-bobbing birds. In the 'M bob(s) per N step(s)' pattern, M bob(s) occurred during N step(s) of walking (M and N are integral numbers). Body movements of these head-bobbing patterns were digitized by Frame Dias software for motion analyses. Digitized body points were the eye, the shoulder, and the tip of the first digit (as previously described by Fujita (2002)). The distal end of the observable portion of the tarsometatarsus segment was digitized when the digits were not observable.

Ground conditions and foraging/non-foraging behavior were also observed. Ground conditions were classified as grassland, flatland, and water. Flatland included sandy beaches, dry sandy areas, and open soil. "Water" indicated that the birds were walking with their feet in the water.

As an indicator of walking speed, step duration was counted (in terms of video frames; 30 frames/sec) and was expressed in seconds. Step duration was counted from one "foot-down" to the next. "Foot-down" was defined in this study as the moment when the entire sole touched the ground. When the feet were hidden in water, grass etc., the moment of foot-down was defined as the moment when the downward movement of the tarsometatarsus segment stopped around the end of the single support phase. A *t*-test was used to compare the mean step duration for each head-bobbing pattern to that for the 'one bob per step' pattern.

RESULTS

Purple Herons, Intermediate Egrets and Japanese

Night Herons generally walked slowly. The mean values of step duration in these three species were greater than one second (see Table 1).

In all nine species, head-bobbing walking was observed during both foraging and non-foraging behaviors. The head-bobbing pattern that was most frequently observed was 'one bob per step' (Table 1). During 'one bob per step', the thrust phase occurred from the double support phase to the beginning of the single support phase (Fig. 1, A–B), and the hold phase was observed from the single support phase to the beginning of the double support phase (Fig. 1, C–D). This pattern was observed in all species.

The second pattern was 'one bob per two steps' which was observed in Purple Herons, Japanese Night Herons and Malayan Night Herons (Table 1). During 'one bob per two steps', the thrust phase started during the double support phase (Fig. 2, A) and continued to the beginning of the single support phase. Then the hold phase started during the single support phase (Fig. 2, B), and continued to the next single support phase (Figs. 2, C–E). Then the thrust phase started again almost simultaneously or immediately after the beginning of the successive double support phase (Fig. 2, F). This pattern was observed when the birds were walking very slowly and looking for prey. The mean step duration of this pattern in Malayan Night Herons was significantly larger than that of the 'one bob per step' pattern ($P < 0.05$). In the Purple Herons, and the Japanese Night Herons, the mean step duration during 'one bob per two steps' was more than three seconds, but did not differ significantly from that during 'one bob per step'.

The third pattern was 'two bobs per step' which was observed only once in the Black-winged Stilt (Table 1). In this pattern, the head movement was similar to that in 'one bob per step', but there was one more short thrust phase during the hold phase (Fig. 3). Thus, two thrust phases and two hold phases occurred during one step. This pattern was observed while the bird walked at normal speed looking for prey.

Non-bobbing walking was observed in the Japanese Night Herons, Pacific Reef Egrets and Gray Herons (Table 1). Whenever Gray Herons were observed non-bobbing walking, individuals were walking on dry sandy ground and were not looking for prey irrespective of their walking speed. The mean step duration of non-bobbing walking was slightly longer than during 'one bob per step' head-bobbing walking, but the difference between them was not

Table 1. Step numbers, ground conditions, and mean and standard deviation of the step duration (sec) for each head-bobbing pattern.

		Total	1 bob 1 step	1 bob 2 steps	2 bobs 1 step	Non-bobbing
Japanese Night Heron	N (nf)	40 (0)	27 (0)	8 (0)	0	5 (0)
	GC	F	F	F		F
	Mean±SD	3.54±1.92	4.03±1.63	3.70±1.87 ^{ns}	—	0.65±0.55**
Malayan Night Heron	N (nf)	72 (0)	68 (0)	4 (0)	0	0
	GC	F/G	F/G	G		
	Mean±SD	0.93±0.85	0.87±0.85	1.83±0.22*	—	—
Cattle Egret	N (nf)	39 (0)	39 (0)	0	0	0
	GC	G	G			
	Mean±SD	0.62±0.32	0.62±0.32	—	—	—
Intermediate Egret	N (nf)	40 (0)	40 (0)	0	0	0
	GC	G/W	G/W			
	Mean±SD	1.54±0.57	1.54±0.57	—	—	—
Little Egret	N (nf)	31 (0)	31 (0)	0	0	0
	GC	W	W			
	Mean±SD	0.54±0.04	0.54±0.04	—	—	—
Pacific Reef Egret	N (nf)	90 (22)	87 (19)	0	0	3 (3)
	GC	F/W	F/W			F
	Mean±SD	0.59±0.13	0.60±0.13	—	—	0.46±0.04 ^{ns}
Gray Heron	N (nf)	60 (52)	18 (10)	0	0	42 (42)
	GC	F/W	F/W			F
	Mean±SD	0.76±0.52	0.64±0.42	—	—	0.81±0.56 ^{ns}
Purple Heron	N (nf)	30 (0)	16 (0)	14	0	0
	GC	G/W	G/W	G		
	Mean±SD	3.74±1.77	4.00±1.92	3.45±1.60 ^{ns}	—	—
Black-winged Stilt	N (nf)	75 (0)	74 (0)	0	1 (0)	0
	GC	W	W		W	
	Mean±SD	0.76±0.45	0.76±0.45	—	1.1	—

Asterisks refer to the statistically significant (**: $P < 0.01$, *: $P < 0.05$, ns: not significant) difference from the mean step duration of the '1 bob 1 step' pattern.

Ground conditions (GC) were exhibited in following abbreviations; F: flatland; G: grassland; W: water.

N: step numbers of both foraging and non-foraging steps; nf: numbers of non-foraging steps.

significant. Japanese Night Herons, however, were observed non-bobbing walking even when walking quickly while foraging. The average step duration of this species while non-bobbing was significantly shorter than during 'one bob per step' ($P < 0.01$). A Pacific Reef Egret was also observed walking without head bobbing while it walked somewhat quickly while not foraging, though the mean step duration of non-bobbing was not significantly different from that of 'one bob per step'.

DISCUSSION

The 'one bob per step' pattern was seen in most of our observations (Table 1) of eight species of herons/egrets and one shorebird. The same pattern

has been observed among other species (Daanje 1951; Bangert 1960; Fujita 2002). In contrast to Dagg's (1977) observations, we found that Pacific Reef Egrets and Black-winged Stilts usually walked in the 'one bob per step' pattern. We also observed 'one bob per two steps' in several species, and 'two bobs per one step' in one species.

The 'one bob per two steps' pattern observed in several heron species (Table 1) had not previously been reported, perhaps because walking herons had not been sufficiently critically observed before. Herons have a longer neck than other birds and can extend it further than other species.

The 'two bobs per step' pattern observed in a Black-winged Stilt seems to be a variation of the typical 'one bob per step' pattern, with one extra short

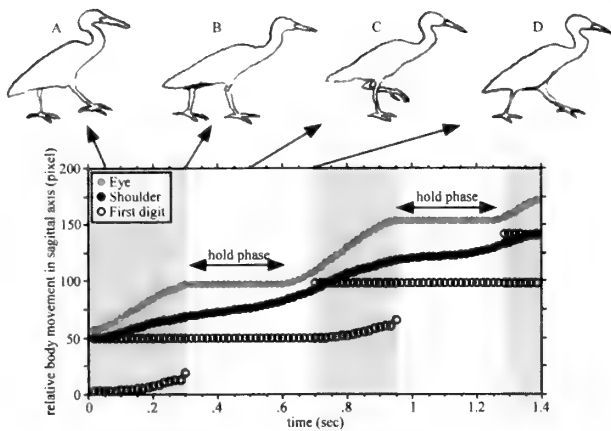


Fig. 1. The 'one bob per step' head bobbing walk of a Pacific Reef Egret. Upper diagrams show body movements traced from a video film of the distinctive phases: A, the thrust phase during the double support phase; B, the hold phase during the double support phase; C, the hold phase during the single support phase; D, the thrust phase during the double support phase. The lower diagram shows the relative horizontal movement of the body points, the eye, shoulder, and first digit, plotted against time. The gray boxes indicate the double support phase during which both feet are on the ground.

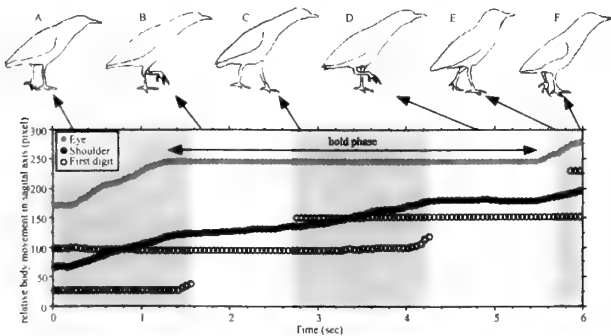


Fig. 2. The 'one bob per two steps' head bobbing walk of a Japanese Night Heron. Upper diagrams show the body movements traced from a video film of the distinctive phases. The first step is from A to C, and the second step is from D to F. The neck is extended during the first double support phase (A-B). The hold phase starts during the first single support phase (B), and continues to the third double support phase (C-E). Then the thrust phase starts again during this double support phase (F). The lower diagram shows the relative horizontal movement of body points, the eye, shoulder, and first digit, plotted against time. The gray boxes indicate the double support phase during which both feet are on the ground.

thrust phase during the hold phase. The bird may have altered the direction of its gaze during this short thrust phase. This pattern has previously been reported for chickens and starlings (scientific names not given) (Dunlap & Mowrer 1930).

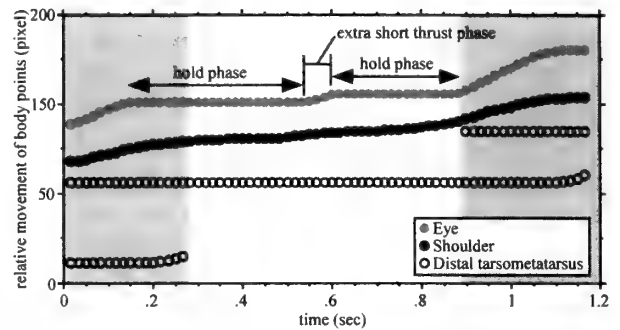


Fig. 3. Relative horizontal movement of the eye, shoulder, and distal tarsometatarsus, during the 'two bobs per step' pattern. Distal tarsometatarsus is defined as the distal end of the observable portion of the tarsometatarsus segment. This was digitized instead of the first digit because the individual walked with its feet in water. The gray boxes indicate the double support phase.

Pacific Reef Egrets and Gray Herons walked without head bobbing when they were not foraging. As these birds were not looking for prey, they may have not needed strict stabilization of the head. Thus, their non-bobbing walking may be indicative of the importance of the visual function of head bobbing when foraging. In the Japanese Night Herons, however, non-bobbing walking was observed when the bird walked quickly while foraging. The reason for its non-bobbing probably differs from that of Pacific Reef Egrets and Gray Herons, and may have been related to its walking speed.

Dagg (1977) reported that White Ibis *Threskiornis molucca* and Bar-tailed Godwit *Limosa lapponica* walked both with and without head bobbing. Three species of herons also walked in both manners in our observations. Pacific Reef Egrets and Black-winged Stilts (classified as non-bobbers by Dagg (1977)), usually head bobbed while walking in our observations. One reason for this inconsistency may be that Dagg (1977) focussed on bobbing behavior and did not record walking speed or foraging behavior. Dagg's (1977) observations of these species may also have been over a small range of walking speeds and under restricted situations. Our observations indicate that non-bobbing walking sometimes occurs when birds are walking at relatively high speeds, or when not foraging.

Dagg (1977) mentioned that most non-bobbing birds generally live near water, and that many head-bobbing birds generally eat seeds or fruits rather than moving prey. In our observations, however, herons and Black-winged Stilts, which live near water and

eat moving prey, usually head bobbed while walking (Fig. 1, Table 1). One of the common characteristics among head-bobbing species seems to be that their foraging behavior consists of looking for food while walking. Comparing many different species of birds that employ different foraging techniques will give more insight into the reasons for head bobbing.

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ORIGINAL ARTICLE

Response to manipulation of partner contribution: A handicapping experiment in the Barn Swallow

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Abstract In birds with biparental care, two parents cooperate to provide the appropriate amount of care for the young. Evolutionary stable strategy (ESS) models predict that cooperation can be stabilized when parents respond to reductions in care by their partners by increasing their effort, while not fully compensating for the reduction. To examine whether parents adjust their effort according to their partner's contribution and what cues the parents use in the bargaining process, we manipulated parental care in the Barn Swallow *Hirundo rustica*. Twenty-eight pairs were randomly assigned to three groups: (i) reduced male parental care (7 pairs), (ii) control (13 pairs), (iii) reduced female parental care (8 pairs). Parental care was manipulated by attaching small weights to the base of a bird's tail feathers. The manipulation successfully reduced parental provisioning in the handicapped birds, while still maintaining biparental care. Regardless of sex, however, handicapping of individuals led to no compensatory responses by the mates. The handicapped birds spent more time resting, causing lowered provisioning rates. Males with a handicapped female decreased their provisioning rates to guard the resting females against extra-pair males. Since the provisioning parents in the three groups seldom met at their nest, it is unlikely that parents monitor their partner's provisioning rate directly. We predicted that parents would adjust their provisioning rates according to the begging behaviors of their nestlings. However, no significant relationship was detected between the begging intensity (begging level and calling duration) and travelling time. Moreover, there were no significant differences in either begging level or calling duration among the three groups. Since various factors affect the provisioning rate in a handicapping manipulation, our data do not support the prediction derived from ESS models of biparental care.

Key words Barn Swallow, Biparental care, *Hirundo rustica*, Parental effort, Weighting manipulation

In species with biparental care, two parents cooperate to provide the appropriate amount of care for the young. The division of labor between mates is best understood as an evolutionary stable strategy (ESS) whose equilibrium depends on the relative costs and benefits of investment to the male and female (Chase 1980; Houston & Davies 1985). Cooperation can be stabilized when parents respond to reductions in care by their partners by increasing their effort, while not fully compensating for the reduction (Houston & Davies 1985). Incomplete partner com-

pensation is a feature of optimal investment strategy (Winkler 1987; Kacelnik & Cuthill 1990), and this prediction is supported by experimental studies in which one partner's contribution is completely removed (Bart & Tornes 1989; Hatchwell & Davies 1990; Markman et al. 1996).

According to the ESS models, parental feeding rates are determined by a bargaining process between parents (Chase 1980; Houston & Davies 1985). The best way to test the process is experimental study in which one partner's contribution is reduced either by clipping a number of feathers (Slagsvold & Lifjeld 1988, 1990; Whittingham et al. 1994; Weimerskirch et al. 1995; Sanz et al. 2000) or by attaching weights to the birds (Wright & Cuthill 1989, 1990a, b; Sæther

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et al. 1993; Markman et al. 1995), and the compensatory response of the partners is then measured. Some experimental studies have supported the ESS models, while others have shown a range of responses to reduced parental care by one partner, from no response through incomplete compensation to complete compensation (see Table 4 in Sanz et al. 2000). Thus, the bargaining process is still obscure and more experiments are necessary to elucidate it.

ESS models of biparental care assume that parents adjust their effort according to their partner's contribution. The bargaining process is possible only if each parent can monitor the behavior of the other. What proximate cues might parents use in the bargaining process? At least three are possible. First, parents may monitor their partner's provisioning rate directly and adjust their effort accordingly. Second, if handicapped partners are spending more time resting near the nest, their mates might monitor resting partners and increase their own provisioning rate. Third, the cue might be nestling behavior, especially begging, rather than parental behavior. Studies on a range of bird species suggest that nestling begging signals regulate the provisioning rate of adult birds (Budden & Wright 2001). If handicapped partners decrease their provisioning rates and nestlings are hungry, nestling begging should be intense and the other partner should increase their provisioning rate. Most experiments have examined the response of the birds to handicapping (e.g. it reduced their provisioning rate), but have not considered the proximate cues that affect parental provisioning rates in the bargaining process.

Our aims with this study are twofold; first, to investigate the responses of male and female Barn Swallows *Hirundo rustica* to experimental tail-weight manipulation of their partners under the same brood size condition, and second, to examine whether parents adjust their effort according to the partner's provisioning rate, the behavior of the handicapped partner, or nestling begging. The Barn Swallow is a suitable organism for this study because nestlings are fed by both parents, which contribute approximately equally, to the raising of young (Møller 1994), and also because it is easy to find their nests and observe nestling behavior.

MATERIALS AND METHODS

1) Study area and population

This study was conducted in a residential area at

Joetsu City, Niigata Prefecture, Japan (37°07'N, 138°15'E, 10 m alt.), in 1997 and 1998. Our study season, from May to June, corresponded to the first breeding period of the swallows. Intensive observation in the week following hatching allowed us to pick a sample from 53 pairs, which nested under the eaves of a covered sidewalk. The average distance between nests was 16.2 m (± 3.4 SE) and both parents cared for the young in each nest. Thus, Barn Swallows in our study area bred in monogamous pairs in a loose colony. Of the 53 pairs, we selected 28 with broods of five chicks for our experiment. Before the experiment, all adults were mist netted, color ringed, and marked with a non-toxic paint on the tail feathers, throat, or forehead to allow individual identification.

2) Weighting experiment

The manipulation designed to produce the reduction in parental provisioning rate was the attachment of small lead weights (each weighing 0.3 or 0.4 g) to the base of the bird's three central tail feathers with quick-drying glue ("Aron alfa", Konishi, Japan). The birds in the experimental groups were weighted with a total of 1.0–1.5 g (approximately 5–8% of their body mass). The nestling period, which is the period from hatching of the last egg to fledging of the last nestling, lasts on average 21 days (Møller 1994). The weighting manipulation was carried out between 0100 and 0300 when chicks were 10 days old. The tail-weighting was temporary, as weights were shed during tail molt at the end of the breeding season. At least 53.3% of the handicapped birds (56.1% for control pairs) started second breeding after the successful fledging of their first broods.

Pairs were randomly assigned to three treatment groups: (i) male parental feeding reduced ($N=7$); (ii) control pairs under natural condition ($N=13$); (iii) female parental feeding reduced ($N=8$). For each pair in the three groups, we recorded the number of provisioning visits per hour using video cameras. We videotaped each nest for at least 2 hours a day, and for at least 2 days between 0600 and 1200. The cameras were placed so that they were aimed up towards the nest at a 45° angle from a distance of 3–5 m. This did not seem to disturb the parents because feeding activities were resumed immediately after we set the video camera in place. Data from all nests were collected using a video cassette recorder, when chick 12–14 days old. When recording parental behavior at nests, we observed their behavior near the nest using

8×30 binoculars for at least 30 minutes. Barn Swallows sometimes perched on electric lines. We regarded perching within 5 m of the nest as resting, and calculated the time budget for resting (percentage of time that individuals spent resting). Fieldwork was performed in fine weather conditions.

3) Encounters between parents

After one parent delivered food to the nestlings, provisioning by the mate usually followed within 1–3 seconds if the mate was ready to visit the nest. In this case, we assumed that the mate could monitor provisioning by the other parent. We defined an encounter between parents at the nest as occurring when the parents took turns at provisioning within 3 seconds or when both parents provisioned simultaneously.

The degree of encounter between parents was calculated using a slight modification of Ekman's (1979) coherence index. This index was defined as:

$$\text{Encounter index (\%)} = \frac{N_c}{N_a + N_b - N_c} \times 100$$

Where N_a and N_b are the numbers of times individuals a and b provisioned, respectively, and N_c is the number of encounters between parents within 3 seconds. If two parents delivered food at the same time in all cases, the encounter index would be 100%.

4) Begging behavior

To quantify begging intensity, we utilized a widely used begging index (e.g. Redondo & Castro 1992). The degree of postural intensity of the begging display was categorized into five levels: the nestling 1) fails to beg; 2) gapes silently while resting on its belly; 3) gapes calling while resting on its belly; 4) gapes calling while elevating its body; and 5) same as 4) plus wing flapping. We estimated the begging level at the time when parents arrived at their nest.

Total parental provisioning rates have been clearly demonstrated to depend on whole-brood begging rates or total noise as a signal of brood demand for food (Budden & Wright 2001). Thus, the begging levels of each nestling in a nest were pooled to give the whole-brood begging intensity. For example, in this study, when each nestling in a nest begged at level 5, the whole-brood begging intensity was 25. From the recorded videotapes, we examined the begging level of each nestling and measured the total calling duration (time from first sound to end of last sound) using a stopwatch.

Parents flew from their nest to a feeding site and then took food home to the nestlings. We defined the round trip as the feeding trip and measured the time spent in each feeding trip as the travelling time. We predicted that parents responded to intense begging or long calling duration would shorten their travelling time.

We were able to measure total calling duration and travelling time in all nests, but begging levels were not examined in 14 out of 28 nests in which we could not monitor the begging behaviors of all five nestlings.

5) Statistical analysis

Each nest was assumed to be a statistically independent observation and parameters (provisioning rate, time spent resting, travelling time and call duration) were normally distributed, so we used a two-way ANOVA to determine the effect of experiment and sex on parameters. When there was a significant interaction in the result of two-way ANOVA, the data were divided into male and female, then a one-way ANOVA was used to compare some parameters among the three treatments. When one-way ANOVA revealed significant differences among treatments, Scheffe's *F*-test was used for post-hoc testing. Nestlings begged several times during a continuous observation period. We used the median of the begging intensity and call duration of a nest as a representative value to minimize bias due to pseudoreplication. To examine the relationship between begging intensity (begging level and calling duration) and travelling time, we used Spearman's correlation coefficient. All statistical procedures were done using StatView 5.0 (SAS 1998).

RESULTS

1) Provisioning rates

The average provisioning rates differed markedly according to the experimental treatment (Fig. 1, two-way ANOVA, $F_{2,50}=18.25$, $P<0.0001$). There was no sex difference in the provisioning rate ($F_{1,50}=0.001$, $P=0.98$), but the interaction between sex and group was significant ($F_{2,50}=17.83$, $P<0.0001$).

One-way ANOVA showed a significant difference in the provisioning rate among the three groups for either male or female (male, $F_{2,25}=15.74$, $P<0.0001$; female, $F_{2,25}=20.17$, $P<0.0001$). The provisioning rate of handicapped males was significantly lower than that of control males (Scheffe's *F*-test,

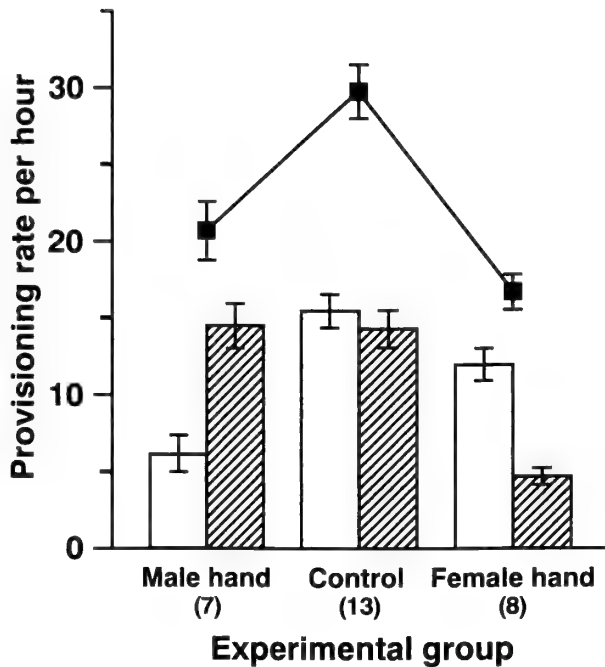


Fig. 1. Average (\pm SE) provisioning rates per hour in the three treatment groups (open bars, males; hatched bars, females). The total provisioning rate per nest for males plus females is depicted above. Sample sizes (number of nests) are given in parentheses.

$P < 0.0001$) and that of males with handicapped females ($P = 0.040$). Likewise, there was a significant difference in the male provisioning rate between the control and female-handicapped groups ($P < 0.05$). The provisioning rate of handicapped females was lowest in the three groups (Scheffe's F-test, $P < 0.0001$). However, there was no significant difference in the female provisioning rate between the male-handicapped and control groups ($P = 0.995$).

The total provisioning rates per nest (top of Fig. 1) differed significantly among the three groups (one-way ANOVA, $F_{2,25} = 15.24$, $P < 0.0001$). Scheffe's F-test revealed a significant difference between the male-handicapped and control groups ($P < 0.01$), and between the female-handicapped and control groups ($P < 0.0001$), but no significant difference between the male- and female-handicapped groups ($P = 0.39$).

2) Encounters between pairs at the nest

The mean encounter index of each group was below 4% (Fig. 2). There was no significant difference in the encounter index among the three groups (one-way ANOVA, $F_{2,25} = 2.49$, $P = 0.10$).

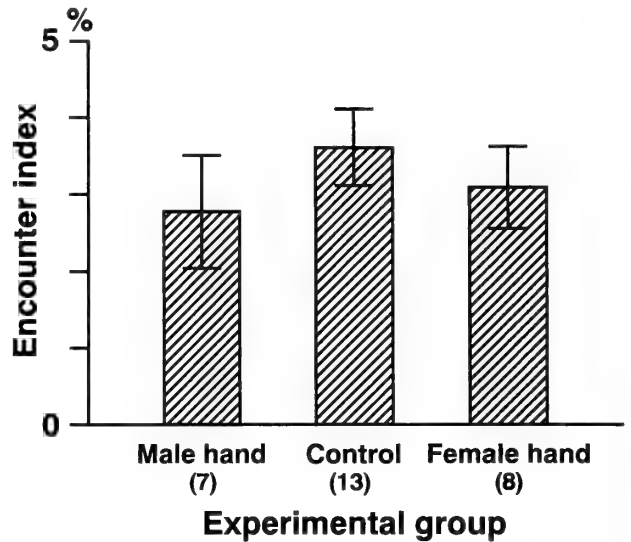


Fig. 2. Average (\pm SE) encounter indices (%) in the three treatment groups. Sample sizes (number of nests) are given in parentheses.

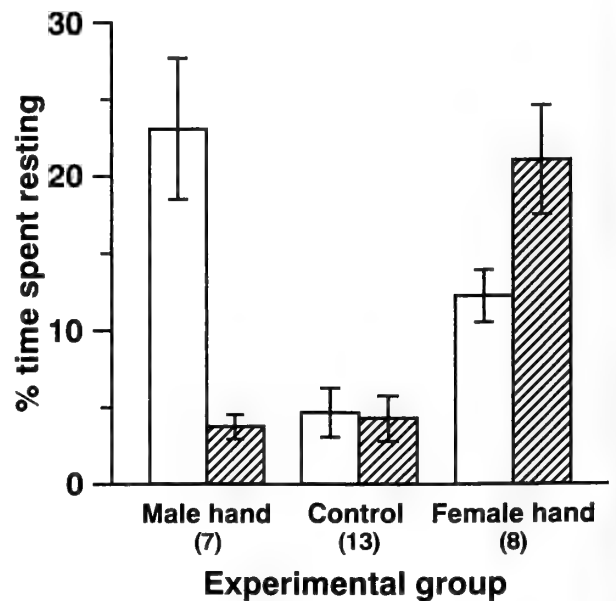


Fig. 3. Average (\pm SE) percentage of time that individuals spent resting within 5 m of the nest in the three treatment groups (open bars, males; hatched bars, females). Sample sizes (number of nests) are given in parentheses.

3) Time spent resting

Two-way ANOVA showed that the effect of treatment on time spent resting was significant (Fig. 3; $F_{2,50} = 16.50$, $P < 0.0001$), as was the interaction between sex and group ($F_{2,50} = 15.22$, $P < 0.0001$). However, there was no sex difference in the time budget ($F_{1,50} = 3.40$, $P = 0.07$).

A significant difference in the time budget was detected among the three groups for both sexes (male, $F_{2,25}=13.45$, $P<0.0001$; female, $F_{2,25}=19.07$, $P<0.0001$). Handicapped males spent more time resting than control males (Scheffe's F-test, $P<0.001$) and than males with handicapped females ($P<0.01$). Males with handicapped females spent more time resting than control males (Scheffe's F-test, $P<0.05$), because they perched close to the resting females. We observed that extra-pair males approached resting females (14 cases); male partners usually chased the extra-pair males away (12 of 14 cases), while we observed extra-pair copulations in the other two cases. Handicapped females spent more time resting than control females (Scheffe's F-test, $P<0.001$) and than females with handicapped males ($P=0.001$), but there was no significant difference between the control and male-handicapped groups ($P=0.87$). Females with handicapped males did not associate with resting males.

4) Response to nestling begging

The average (\pm SE) travelling time of males and females was 277.2 (\pm 12.5, $N=757$) and 230.0 (\pm 10.1, $N=841$) seconds, respectively (data were pooled for all individuals). No significant relationship was found between the begging level and travelling time in 14 males ($P>0.05$ for 4 handicapped males, 4 control males and 6 males with handicapped females) and 14 females ($P>0.05$ for 4 females with handicapped males, 4 control females and 6 handicapped females): male and female parents did not shorten their travelling time as begging level increased. Likewise, there was no significant relationship between call duration and travelling time in 28 males ($P>0.05$ for 7 handicapped males, 13 control males and 8 males with handicapped females) and 28 females ($P>0.05$ for 7 females with handicapped males, 13 control females and 8 handicapped females).

Regardless of treatment or sex, the average begging intensity of the entire brood was ca. 19 (Fig. 4). Two-way ANOVA showed no significant effect of either treatment ($F_{2,22}=0.99$, $P=0.39$) or sex ($F_{1,22}=0.26$, $P=0.62$) on begging intensity and no significant interaction between the two variables ($F_{2,22}=0.29$, $P=0.75$). This was because almost all the nestlings begged at level 4. We obtained data on 5,180 begging episodes from 70 nestlings. Begging at level 4 accounted for 84.5% (4,377) of the cases (level 1, 2.3%; level 2, 3.7%; level 3, 8.3%; level 5, 1.2%).

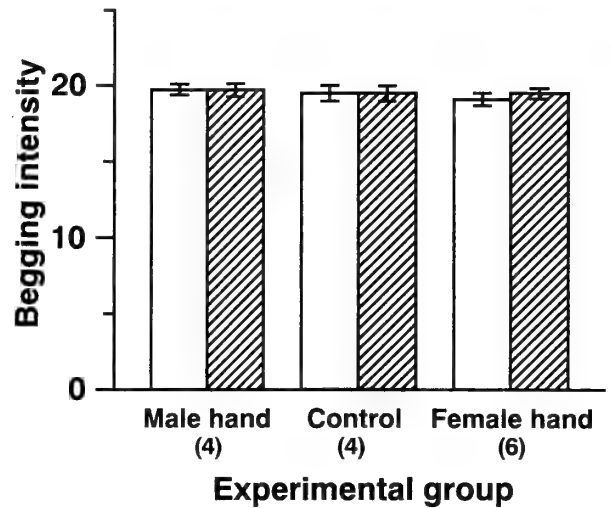


Fig. 4. Average (\pm SE) whole-brood begging intensity in the three treatment groups (open bars, males; hatched bars, females). Sample sizes (number of nests) are given in parentheses.

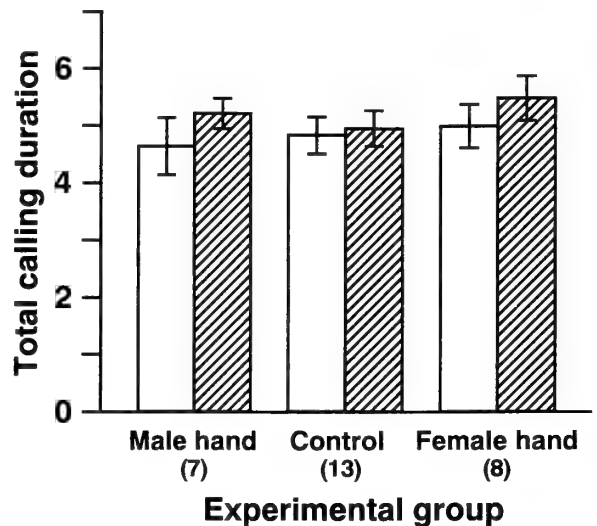


Fig. 5. Average (\pm SE) total calling duration (seconds) in the three treatment groups (open bars, males; hatched bars, females). Sample sizes (number of nests) are given in parentheses.

Regardless of treatment or sex, nestlings begged for about 5 seconds (Fig. 5). The average total call duration did not differ according to the experimental treatment (two-way ANOVA, $F_{2,50}=0.54$, $P=0.58$). Likewise, there was no sex difference in call duration ($F_{1,50}=1.70$, $P=0.20$) and no significant interaction between sex and group ($F_{2,50}=0.26$, $P=0.77$).

DISCUSSION

In our experiments, manipulation successfully reduced parental provisioning by handicapped birds, while still maintaining a biparental system (Fig. 1). Regardless of sex, however, handicapping of individuals led to no compensatory responses from their mates (Fig. 1). Previous handicapping experiments in passerines have shown compensatory responses by males or females (Sanz et al. 2000), so our results are exceptional. The low encounter index shows that provisioning parents seldom meet at the nest. Therefore, it is unlikely that parents monitor their partner's provisioning rate directly. No significant relationship was detected between begging intensity (begging level and calling duration) and travelling time. There were no significant differences in either begging intensity or calling duration among groups (Figs. 4 & 5). It is unclear whether parents adjust their provisioning rates according to nestling behavior.

Handicapped females spent more time resting near the nest, thereby decreasing their provisioning rates (Figs. 1 & 3). Before and after males visited their nests for provisioning, they were able to see their resting females. However, male swallows with handicapped females did not increase their provisioning rates. While females were resting, extra-pair males attempted to copulate with them but were chased off by their male partners. Colonial breeding species have a high frequency of extra-pair copulation (Birkhead & Møller 1992). Møller (1987a, b) found that Barn Swallow females in colonies, where the likelihood of extra-pair copulation is greater, tend to be guarded more closely than females of solitary pairs. Barn Swallows in our study area bred in a loose-colony. Thus, it is reasonable to suppose that males decreased their provisioning rates to guard their resting females. Wright and Cuthill (1989, 1990a, b) manipulated the parental care of the European Starling *Sturnus vulgaris* in a nestbox colony and found that, regardless of sex, the provisioning rate was reduced in handicapped birds with an incomplete compensatory increase by their unmanipulated partner. However, they did not report on the resting of handicapped females or on mate guarding.

Females with handicapped males did not increase their provisioning rates as a result of their partners' lower provisioning rate (Fig. 1). It is unclear whether this is because handicapped females could not work harder due to an upper limit on energetic expenditure (Drent & Daan 1980), or whether handicapped fe-

males maintained the frequency of their feeding visits by switching prey types. Parental care in terms of food delivered to the nest depends not only on the provisioning rate, but also on what is delivered (Whittingham et al. 1994). Starling parents maintained their provisioning rates by switching prey types to those that were more quickly gathered or to smaller prey types (Wright & Cuthill 1989, 1990a, b). Compensation by switching prey types may be true of the male swallows with handicapped females as well as the females with handicapped males. Unfortunately, we have no data on food items.

The total provisioning rates of the manipulated groups were lower than those of the control groups (Fig. 1). We expected that the low provisioning rates lead to an increase in nestling hunger level and nestling begging intensity. The more frequent begging is or the larger begging call is, the more parents provision their nestlings (Budden & Wright 2001). Our data did not show this trend, however, and parents did not shorten their travelling time as begging level increased. Moreover, most nestlings in each group begged at level 4. There are at least two possible reasons for this. First, the nestlings may always be hungry, even if the parents provision at a high rate. Saino et al. (2000) demonstrated in Barn Swallows that begging behavior is a signal of need (the amount of resources requested by an offspring to achieve satiation). Begging at level 4 when chicks are 12–14 days old seems to achieve the maximum level and reflect their need level. Another possible reason is the shortness of the period of observation. We could not collect long-term data because many chicks in our study nests were predated by the Carrion Crows *Corvus corone* after chicks were 15 days old. Some previous experiments have shown that compensation requires a longer time to be effective. For example, Wright and Cuthill (1989) collected data for starling chicks between 11 and 20 days of age, and their results showed compensatory responses by males and females. Long-term manipulation may lead to an increase in nestling hunger level and nestling begging intensity.

Although our study presents negative data for ESS models of biparental care, we can not assert that partners with handicapped mates do not show any compensation. The provisioning rate by each partner is affected by many factors (age, sex and number of chicks, parent-offspring relatedness, conditions of parent and offspring, time of season, and paternity). In this study, we limited ourselves to the response of

a parent to its partner's contribution. However, many factors affect the provisioning rate in a handicapping manipulation. Is mate-guarding for handicapped females always found? Do parents maintain the frequency of their visits by switching prey types? Does long-term manipulation lead to an increase in levels of nestling hunger? Moreover, recent studies indicate that there are sex differences in responsiveness to begging signals (Kilner 2002; Macgregor & Cockburn 2002). Further research on these points is needed to assess our experimental results more precisely.

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SHORT COMMUNICATION

Low prevalence of blood parasites in five Sylviidae species in Japan

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About 450 species of blood parasites have been recorded from nearly 4,000 sampled bird species (Bishop & Bennett 1992). Due to their potential detrimental affects on the reproduction and survival of different bird species (e.g. Sundberg 1995; Dufva 1996), blood parasites are gaining increasing prominence (McCallum & Dobson 1995; Sodhi 1995; Dale et al. 1996). Before blood parasites can be used for various rigorous ecological studies, it is an important first step to determine the level of prevalence of blood parasites in various species. We determined the prevalence of five blood parasites (*Haemoproteus* spp., *Trypanosoma* spp., *Splendidofilaria* spp., *Plasmodium* spp. and *Leucocytozoon* spp.) in five Sylviidae species (*Cisticola juncidis*, *Locustella pryeri*, *L. pleskei*, *Acrocephalus arundinaceus*, and *A. bistrigiceps*) in Japan.

Previously we found that seven *Emberiza* species have low blood parasite presence in three of the study sites, Kamisu, Ukishima, and Seimei (Sodhi et al. 1996; Sodhi et al. 1999). Only three species, *E. rustica*, *E. spodocephala* and *E. schoeniclus*, were infected with a blood parasite. We also examined four Sylviidae species inhabiting reedbed and the Styan's Grasshopper Warbler (*L. pleskei*) inhabiting dwarf laurel forest that is a congener to the endangered Japanese Marsh Warbler (*L. pryeri*).

We sampled warblers at three sites within Japan, Kamisu (35°51'33"N, 140°38'20"E) along lower Tone River, Ukishima (35°57'N, 140°28'E) and Funako (36°01'N, 140°16'E) along Lake Kasumigaura, and Ohtsukuejima (33°40'N, 130°18'E). At each site, warblers were caught using mist nets in the breeding season of 1996 and 1997. From some of the caught warblers, we collected a small amount of blood by

puncturing the brachial vein, and released them after measuring and taking blood samples. Blood smears were prepared by using the method described by Clayton and Moore (1997) and were air-dried and fixed in 100% ethanol. The blood smears were stained using Giemsa's stain. The presence of blood parasites was determined for each blood smear by examining 100 randomly selected fields under a 100x oil immersed objective (see Bennett et al. 1995 for details).

A total of 252 individuals belonging to five warbler species were examined for the prevalence of blood parasites. Only 2 (0.8%) individuals of the Great Reed Warbler were infected with *Plasmodium* sp. (Table 1). Because only early developing gametocytes were found, the blood parasites could not be identified to specific level.

Between 1965 and 1971, of 425 individuals examined belonging to 27 bird species from Tsunoshima island, Yamaguchi Prefecture (34°21'N, 130°51'E), 53 (12%) were infected with a blood parasite (McClure et al. 1978). On this island, three species of *Phylloscopus* warblers were examined. Twenty-two Crowned Willow Warblers (*P. coronatus*) were free of blood parasites. Only one of 52 individuals examined of the Arctic Warblers (*P. borealis*) and one of 27 individuals examined of the Pale-legged Willow Warblers (*P. borealoides*) were infected with a blood parasite from this area.

The present study and previous reports (McClure et al. 1978; Sodhi et al. 1996; Sodhi et al. 1999) show that in general the blood parasite prevalence is low in warbler and bunting species in Japan. Both migratory and resident species had low blood parasite prevalence (Table 1, Sodhi et al. 1999). It is unclear what the possible mechanisms are that help birds to maintain a relatively low prevalence of blood parasites in this region. Low prevalence of blood parasites found

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Table 1. The number of individuals sampled for the presence of blood parasites in five species of warblers in Japan.

	Sampling sites								
	Kamisu Ibaraki			Lake Kasumigaura Ibaraki			Ohtsukue-jima Fukuoka		
	M	F	U	M	F	U	M	F	U
Resident species									
Fan-tailed Warbler, <i>Cisticola juncidis</i>	2	1	—	12	10	2	—	—	—
Japanese Marsh Warbler, <i>Locustella pryeri</i>	26	4	1	5	7	8	—	—	—
Migratory species (Summer visitor)									
Styan's Grasshopper Warbler, <i>L. pleskei</i>	—	—	—	—	—	—	1	1	9
Great Reed Warbler, <i>Acrocephalus arundinaceus</i>	2	1(1)	1	41(1)	21	4	—	—	—
Black-browed Reed Warbler, <i>A. bistrigiceps</i>	10	—	—	20	30	19	—	—	—

The number of individuals infected is indicated in parentheses. F=female, M=male, and U=unknown sex.

by us may be due to several reasons such as the lack of a suitable arthropod vector (e.g. mosquitoes), host specificity in available arthropod vector, and/or lack of blood parasite susceptibility. It is also possible that the examined birds had latent infections that are difficult to detect. Species of avian *Plasmodium* have much broader host specificity than *Haemoproteus* or *Leucocytozoon* and may infect coexisting species beyond avian families (Atkinson & van Riper 1991). From a conservation perspective, it is probably much easier for maintaining the local population of endangered Japanese Marsh Warbler and vulnerable Japanese Reed bunting because the coexisting species have less prevalence of blood parasites.

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A List of Referees 2002

The editors of Ornithological Science extend hearty gratitude to the referees, who kindly and voluntarily helped the advancement of ornithology. The figures in parentheses denote the number of papers they refereed.

Mitsuhiko ASAKAWA, Kazuhiro EGUCHI, Yuzo FUJIMAKI, Masahiro FUJIOKA, Shoji HAMAO, Mitsuhiko HAYASHIDA, Teruaki HINO (5), Masanobu HOTTA (2), Sadao IMANISHI, Ken ISHIDA, Akiko KATO, Noritomo KAWAJI, Kazuto KAWAKAMI, Kimiya KOGA, Yohsuke KOMINAMI, Reiko KUROSAWA, Hajime MATSUBARA, Hiroshi MOMOSE, Masashi MURAKAMI, Hiroshi NAKAMURA, Kazuo NAKAMURA, Masahiko NAKAMURA, Sumio NAKAMURA, Isao NISHIUMI, Nariko OKA, Yuichi OSA, Yasuyuki SAITO, Hidetsugu SAKAI, Shigeho SATO, Tetsuro SHIMADA, Masaoki TAKAGI (2), Hitoshi TOJO, Yukihiro TOKUNAGA, Keisuke UEDA (3), Eiichiro URANO, Takeshi WADA, Yutaka WATANUKI, Ken YODA, Hoshiko YOSHIDA

Rewriter: Mark BRAZIL

Abstracts of the Japanese Journal of Ornithology, Volume 51

Number 1

ARTICLES

Aims of the basic researches of Great Cormorant (*Phalacrocorax carbo*), assessment of its impact and the damage control.

Masae NARUSUE and Hisashi SUGAWA

The Great Cormorant (*Phalacrocorax carbo*), a high-trophic level consumer in the wetland ecosystem, nests in the colonies sometimes in urban areas. Recent expansion of its distribution and the increase of the population size are presumably attributed to the changes both of the human activities and the wetland ecosystems in Japan. The Great Cormorants occurred widely throughout Japan before 1940, then both their ranges and numbers decreased, so that by the beginning of the 1970s this species was considered as threatened. Subsequently, however, the population size has increased gradually, then during the 1990s the population underwent rapid increase in numbers and spread widely. As a consequence, they gave impacts on forests where they nest and inland fisheries. In order to assess the extent of the current impacts and to control the damage, the four meetings were

held between 1998 and 2001 during the annual meeting of the Ornithological Society of Japan. The meetings were steered by cormorant researchers, in which the coexistence of people and Great Cormorants was discussed. The special issues in this volume summarise the results of these meetings.

Jpn J Ornithol 51: 1–3. 2002.

Changes in the distribution and abundance of the Great Cormorant *Phalacrocorax carbo* in Japan.

Michio FUKUDA, Masae NARUSUE and Nanae KATO

The distribution and abundance of the Great Cormorant *Phalacrocorax carbo* in Japan have changed markedly. Before 1920 cormorants were widely distributed throughout Japan south of Hokkaido. From the end of 19th century to 1940s, cormorants decreased rapidly because of illegal hunting. After 1945, the expansion of human activities, development, and water pollution were the causes of further decreases in the cormorant population and range. In 1971, fewer than 3,000 cormorants bred in just three colonies in Japan. From the late 1970s onwards, numbers of cormorants gradually began to increase; they formed sub-colonies or roosts in areas close to these

three colonies. The main reasons for this increase are assumed to have included improvements to freshwater quality, progress in freshwater purification (which led to increased fish stocks), and reduced disturbance of cormorants by people. During 1980s cormorants began to disperse widely due to the culling for pest control in Aichi, Gifu and Mie prefectures. At present, there are an estimated 50,000–60,000 Great Cormorants in Japan, occurring from Oita prefecture in the south, to Aomori prefecture in the north.

Jpn J Ornithol 51: 4–11. 2002.

Diet and foraging site selection of the Great Cormorant in Japan.

Kayoko KAMEDA, Takeshi MATSUBARA, Hiroshi MIZUTANI and Yoshihiro YAMADA

During the 1990s, the number of Great Cormorant (*Phalacrocorax carbo*) in Japan has been increasing. As a consequence, there have been increasing conflicts between cormorants and fresh water fisheries. We reviewed the species and size range of fish eaten by cormorants, examined their food requirements, and foraging site selection in the Kanto, Tokai, and Kansai areas of Honshu. Cormorants eat various fish species from fresh, brackish, or marine waters, depending on seasonal changes in food availability in each habitat. Cormorants generally eat fish measuring 3–30 cm in length. Each individual cormorant requires approximately 500 g of fish each day. Individual differences in foraging site selection were indicated by stable isotope analysis. A greater understanding of the foraging ecology of cormorants is necessary in order to manage the population and/or behaviour of this piscivorous bird effectively.

Jpn J Ornithol 51: 12–28. 2002.

A review of studies on effects of the Great Cormorant (*Phalacrocorax carbo hanedae*) colonies and roosts on forest ecosystem.

Akira ISHIDA

The present paper reviews current knowledge on the effects of Great Cormorant (*Phalacrocorax carbo hanedae*) nesting and roosting on forest ecosystems. The intensity of their effects was considered dependent on the duration of their residence and their activity levels in forests. Field surveys and experimental studies showed that both plants and soils beneath colonies and roosts are affected by the deposition of feces, and damage to twigs and foliage (caused by flapping and trampling, and by collection for nest ma-

terials). These activities may change the interactions among plants and between plants and soil, and may affect the community structure of soil animals and fungi. This change of the interactions among biological/chemical and physical factors resulted in the changes of the succession of the plant communities. The mechanism causing the decline and death of plants, the succession of forest vegetation, the dynamics of plant community structure and biological interactions in the cormorant colonies and roosts are still unclear. A greater understanding of the basic ecological implications of cormorant nesting and roosting is essential in order to have management strategies for reducing damage on forests by cormorants.

Jpn J Ornithol 51: 29–36. 2002.

The current status of dioxin pollution and its intrinsic effects on Great Cormorants (*Phalacrocorax carbo*) in Japan: an overview.

Naomasa ISEKI, Jun HASEGAWA, Shin-ichi HAYAMA and Shigeki MASUNAGA

In this paper we outline the history of toxic contaminants in wild birds in Japan. Pollution by dioxin and dioxin-like compounds has become a common issue in recent decades. As such pollution poses a considerable health problem, countermeasures and technology to reduce the impacts are important. Very few papers have so far focussed on the effects of dioxin and dioxin-like compounds on wild life in Japan. For the purposes of our research, we selected the Great Cormorant (*Phalacrocorax carbo*). This fish-eating species nests colonially, and can be regarded as an indicator species of the effects of dioxins and dioxin-like compounds. We monitored cormorant health and compared it with published information on other. The cormorant residue levels were found to be higher than among other birds. The residue of PCDD/Fs consisted mainly of 2,3,7,8-substitution, in which 1,2,3,7,8-PeCDD and 2,3,4,7,8-PeCDF were the greatest contribution to toxic equivalency (TEQ). These compounds are accumulated more in the liver than egg and muscle. Based on the half-lives of dioxin and dioxin-like compound in the body of the cormorants, a decadal change of pollutant levels of their eggs was calculated using that of the environmental. It seems likely that embryo mortality, caused by dioxins, was the main toxic effect during the 1970s, but this declined dramatically over the following decades. We conclude that the estimated embryo mortality caused

by PCDD/Fs and co-PCBs pollution (27%) was so small and would not impact population status. However, studies of the other end points such as LOEL of enzyme activity and immunotoxicity are still needed. Our sample size was small and it is desirable to monitor large number of birds with unlethal techniques.

Jpn J Ornithol 51: 37–55. 2002.

Policy for the management of the Great Cormorant in Japan.

Shin-ichi HAYAMA

The Great Cormorants (*Phalacrocorax carbo*) have recently gave impacts on forestry and fishery in Japan. To decrease the population of this species, culling was operated in many locations, which appeared not to be so effective. These human-cormorant conflicts have not been mitigate easily because so many factors are contributed. The special animal management planning system will be applied in the future under the Wildlife Protection and Hunting Law.

Jpn J Ornithol 51: 56–61. 2002.

The home range and flock size of the Azure-winged Magpie *Cyanopica cyana* during the non-breeding season in Nagano Prefecture.

Sadao IMANISHI

The home ranges and flock sizes of the Azure-winged Magpie *Cyanopica cyana* were studied during the non-breeding season in the Ina area (ca. 800 m alt.) from 1977 to 1981 and in the Nobeyama area (ca. 1350 m alt.) from 1980 to 1983 in Nagano Prefecture, central Honshu, Japan. The climate of the Nobeyama area was more severe in winter than in the Ina area. In the Ina area, the average home range size of ten flocks was 135.1 ha, while in the Nobeyama area five flocks average home ranges of 287.6 ha. The fall, winter and spring ranges of one flock in Ina area almost completely overlapped, but the range of the single flock at Nobeyama area expanded during winter and contracted in spring. The home ranges of neighboring flocks partly, or largely overlapped. The average size of ten flocks at Ina was 28.7 birds, while the average of five flocks at Nobeyama was 16.4 birds. The size of the Ina flock decreased over time, but that of Nobeyama remained the same. Population density was 9.6 birds/at Ina and 4.2 birds/at Nobeyama. Flock sizes in both areas were unstable during October, and decreased gradually from November to April. The flock size was reduced from October to April by the

rate of 33.5% at Ina and 31.4% at Nobeyama, respectively. The difference in the home ranges of the flocks in the two areas may result from environmental factors such as weather conditions and food availability during winter.

Jpn J Ornithol 51: 62–73. 2002.

The biology of Hazel Grouse *Bonasa bonasia*.

Yuzo FUJIMAKI

The Hazel Grouse (*Bonasa bonasia*) is a small forest grouse occurring in temperate and boreal forests from Scandinavia to the Far East. The species is assumed to have reached Hokkaido, northern Japan, via Sakhalin Island, during the last ice age about 40,000 years ago. The subspecies occurring in Hokkaido is now recognisably distinct as *B. b. vicinitas*. Pairs are formed from late March to early May. During this period males whistle actively. Six to ten eggs are laid in early or mid-May and hatch in early June after incubation of 23 to 25 days. Young attain adult size by late August and have adult plumage by mid-September. The main diet consists of the leaves and seeds of herbaceous plants and trees and arthropods during late spring and summer, the buds of broad-leaved trees and vine fruits during autumn and winter, and buds and catkins in early spring. The Hazel Grouse has two large caeca supporting effective digestion of the plant fibers comprising their main diet. Hazel Grouse prefer broad-leaved and mixed forests with relatively dense undergrowth, and they avoid larch plantations in Hokkaido. Recently, the Hazel Grouse population has decreased in Hokkaido, the main cause of which is considered to be predation by the red fox (*Vulpes vulpes*), which increased in numbers from the early 1970s until the 1990s. Brood sizes were smaller during low population periods than during normal population periods. In order to maintain, or increase, Hazel Grouse population levels, habitat management and predator control is considered necessary.

Jpn J Ornithol 51: 74–86. 2002.

SHORT NOTE

The first captured record of Willow Warbler *Phylloscopus trochilus* from Japan.

Hisashi NAGATA, Hisahiro TORIKAI and Takema SAITOH

Jpn J Ornithol 51: 87–91. 2002.

Number 2

ARTICLES

Seed dispersal of *Styrax japonica* by Varied Tits *Parus varius* on Miyake-jima, Izu Islands.

Hiroshi HASHIMOTO, Takashi KAMIJYO and Hiroyoshi HIGUCHI

Dispersal of *Styrax japonica* (a deciduous tree) seeds by Varied Tits *Parus varius* was observed on Miyake-jima, Izu Islands. Seven sample trees were monitored for 65–780 min. to examine seed consumption by birds. Varied Tits visited all the sample trees and carried off some of the fruits. The tits removed the toxic pulp and testae from the *S. japonica* fruits using their bills, and ate only the seed albumen. The tits stored some of the seeds close to the trees, but carried many others out of sight. Half of the stored seeds were placed on the ground, and these seeds presumably had a chance of germination, thus the Varied Tit may be an important seed disperser of *S. japonica* on Miyake-jima.

Jpn J Ornithol 51: 101–107. 2002.

Effects of brood size on chick growth and survival in early and late breeding Black-tailed Gulls in two years of different environmental conditions.

Kenichi ISEKI and Yutaka WATANUKI

To examine the effects of brood size on chick growth and survival, we manipulated the brood size of early and late breeding Black-tailed Gulls (*Larus crassirostris*) that usually lay two eggs, in two years of different environmental conditions at Rishiri Island, Hokkaido. Early breeders produced more chicks that grew faster than late ones, though there were no significant interactions between the effects of laying period and brood size. In 2000, the parents of enlarged 3-chick-broods produced greater number of 25-day-old chicks than those of reduced 1-chick-broods. In 2001 with heavy rain, however, the effects of brood size on the number of 25-day-old chicks were not sig-

nificant because the survival of 3-chick-broods was small. This indicated that the parents might not be able to care three chicks during bad weather. Body mass of chicks at 25-day-old was smaller for larger broods in both early and late breeders and in both years. In our study, parents might not have enough ability to provision three chicks.

Jpn J Ornithol 51: 108–115. 2002.

Breeding biology of the Great Cormorant *Phalacrocorax carbo* in Japan.

Michio FUKUDA

Great Cormorants *Phalacrocorax carbo* breed year round in Japan, though there are variations between colonies in the timing and duration of breeding. Males bring more nesting material than females do. The clutch consists of 2–3 eggs and both male and female parents alternate incubation duties for a month. At the Shinobazu Pond colony, Tokyo, the chicks of nests on trees fledged in 31–59 days (average 45 days). Although essentially monogamous the cormorants often mate with other partners even during the same breeding season. At the Shinobazu Pond colony, males start to breed at a younger age (1–6 years-old, average 2.1 years) than females (1–8 years-old, average 2.6 years).

Jpn J Ornithol 51: 116–121. 2002.

SHORT NOTE

The first record of the Rose-coloured Starling *Sturnus roseus* from Okinawa Prefecture.

Satoshi TOKOROZAKI, Kaori TOKOROZAKI and Eiki SUNAGAWA

Jpn J Ornithol 51: 122–124. 2002.

TECHNICAL REPORT

A device to inspect woodpecker cavities.

Shigeru MATSUOKA

Jpn J Ornithol 51: 125–128. 2002.

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4) References

References in the text:

Tokugawa (1995) or (Tokugawa 1995)

Oda and Smith (1996) or (Opel & Smith 1996)

Mori et al. (1997) or (Mori et al. 1997; Richard et al. 1999a)

Journals:

Yamaguchi N & Kawano KK (2001) Effect of body size on the resource holding potential of male varied tits *Parus varius*. Jpn J Ornithol 50: 65–70.

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Cambell RC (1974) *Statistics for biologists*. 2nd ed. Cambridge Univ Press, London.

Chapters in a book:

Dawson WH (1996) Energetic features of avian thermoregulatory responses. In: Carey C (ed) *Avian energetics and nutritional ecology*. pp 85–124. Capman & Hall, New York.

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Yamagishi S (1981) *Možu no yomeiri — toshikouen no mozu noseitai wo saguru* (The bridal of shrikes — ecological research of bull-headed shrikes in an urban park). Dai-Nippon-Tosho, Tokyo (in Japanese).

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ORNITHOLOGICAL SCIENCE

Volume 2 Number 1 February 2003

Contents

SPECIAL FEATURE

Ecology of seed dispersal

Ueda K

Introduction.

1

**Kominami Y, Sato T, Takeshita K,
Manabe T, Endo A & Noma N**

Classification of bird-dispersed plants by
fruiting phenology, fruit size, and growth
form in a primary lucidophyllous forest:
an analysis, with implications for the
conservation of fruit-bird interactions.

3

Takanose Y & Kamitani T

Fruiting of fleshy-fruited plants and
abundance of frugivorous birds: Phenological
correspondence in a temperate forest in
central Japan.

25

Hayashida M

Seed dispersal of Japanese stone pine by the
Eurasian Nutcracker.

33

Fukui A

Relationship between seed retention time in
bird's gut and fruit characteristics.

41

**Rakotomanana H, Hino T, Kanzaki M &
Morioka H**

The role of the Velvet Asity *Philepitta*
castanea in regeneration of understory shrubs
in Madagascan rainforest.

49

ORIGINAL ARTICLES

Fujita M & Kawakami K

Head-bobbing patterns, while walking, of
Black-winged Stilts *Himantopus himantopus*
and various herons.

59

Tajima K & Nakamura M

Response to manipulation of partner
contribution: A handicapping experiment in
the Barn Swallow.

65

SHORT COMMUNICATION

Nagata H & Sodhi NS

Low prevalence of blood parasites in five
Sylviidae species in Japan.

73

A List of Referees 2002

75

**Abstracts of the Japanese Journal of
Ornithology, Volume 51**

75

HIST

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Election Results of President and Executives

日本鳥学会会長・評議員選挙結果

日本鳥学会選挙管理委員会 佐藤恵 濱尾章二 松田道生

任期 2004 年 1 月 1 日～2005 年 12 月 31 日
選挙期間 2003 年 10 月 13 日～2003 年 11 月 12 日
開票日 2003 年 11 月 14 日
開票場所 日本大学歯学部
有権者数 1005 人

1. 会長選挙 投票総数 250(投票率 24.9%), 有効投票 248, 無効投票 2(内、白票 1)

開票結果

候補者 樋口 広芳 HIGUCHI, Hiroyoshi 信任 243 票 (信任当選)
不信任 5 票

2. 評議員選挙 投票総数 193(投票率 19.2%), 有効投票 139, 無効投票 54(内、白票 20)

開票結果 (得票同数は五十音順)

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3. 山岸 哲	YAMAGISHI, Satoshi	59	当選、就任承認
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6. 藤岡 正博	FUJIOKA, Masahiro	55	当選、就任承認
7. 唐沢 孝一	KARASAWA, Koichi	53	当選、就任承認
8. 江崎 保男	EZAKI, Yasuo	47	当選、就任承認
9. 中村 雅彦	NAKAMURA, Masahiko	43	当選、就任承認
10. 川路 則友	KAWAJI, Noritomo	41	当選、就任承認
11. 江口 和洋	EGUCHI, Kazuhiro	38	当選、就任承認
11. 尾崎 清明	OZAKI, Kiyoaki	38	当選、就任承認
13. 永田 尚志	NAGATA, Hisashi	35	当選、就任承認
14. 阿部 學	ABE, Manabu	33	当選、就任承認
15. 綿貫 豊	WATANUKI, Yutaka	32	次点
樋口 広芳	HIGUCHI, Hiroyoshi	19	会長当選

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- ・ 上記票のほか、締め切り後の到着が 1 通ありました。

副会長・常任評議員の選出

日本鳥学会事務局

上記役員選挙の結果にもとづき、次期評議員の間で検討した結果、次期の副会長と常任評議員には以下の方々選ばれました。

任期は評議員と同じく 2004 年 1 月 1 日から 2005 年 12 月 31 日までです。

副会長 中村 浩志 NAKAMURA, Hiroshi

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INVITED ARTICLE

Adaptations and maladaptations to island living in the Seychelles Warbler

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Abstract The Seychelles Warbler (*Acrocephalus sechellensis*) was an endangered endemic of the Seychelles islands where, until 1988, the entire population of ca. 320 birds was restricted to the one island of Cousin Island (29 ha). Although warblers can breed independently in their first year, some individuals remain in their natal territory as subordinates, and often help by providing nourishment to non-descendent offspring. The frequency of helping is affected by habitat saturation, variation in territory quality (insect prey availability), and the genetic relatedness between the helper and the offspring. Helping results in indirect benefits from enhancing the reproductive success of close relatives, and direct benefits as improved parental skills and the acquisition of parentage. The overall helping benefits are higher for daughters than for sons, and it is therefore no wonder that most helpers are daughters from previous broods. Furthermore, on low-quality territories breeding pairs raising sons gain higher fitness benefits than by raising daughters, and vice versa on high-quality territories. Female breeders adaptively modify the sex of their single-egg clutches according to territory quality: male eggs on low quality and female eggs on high quality. However, despite the saturated nature of the Cousin population, the possibility of obtaining higher reproductive success on new nearby island, and a well developed flight apparatus, inter-island dispersal by Seychelles Warblers is extremely rare. The Seychelles Warbler is a beautiful example of behavioural and life history adaptations and maladaptations to restricted circumstances.

Key words Co-breeding, Competition, Cooperative breeding, Fitness benefits, Seychelles Warbler, Territory inheritance

The evolution of flight was a major innovation for birds and insects, permitting them to disperse from inhospitable sites, to exploit habitats unavailable to terrestrial predators and to forage in three dimensions and over very large areas. Some island species, however, refuse to disperse to other relatively close suitable islands despite the fact that they are capable of sustained flight (Diamond 1981; Raikow 1985). Other island species cannot disperse to other islands, because they have lost their flight capacity. The capacity to fly is an energetically costly affair as the muscles that constitute the flight apparatus of birds represent 17 to 25% of body mass (Greenewalt 1975), and the metabolic demands of these special-

ized flight muscles rank among the highest of all tissues (e.g., Weber & Piersma 1996). It therefore comes as no great surprise that under particular ecological conditions some species of bird and insect have lost their morphological flight capacity (e.g., Diamond 1981; Livezey 1992a,b; Trewick 1997). The majority of flightless species live on islands with low resource availability and without mammalian predators. As the capacity to fly is costly (Greenewalt 1975; Weber & Piersma 1996), the loss of flight may be a consequence of selection for reduced energy expenditure in the face of intra-specific competition for food, or because the benefits of flight (*viz.* predator escape) no longer apply in these habitats (e.g. Roff 1990, 1994; Wagner & Liebherr 1992; McNab 1994a,b). However, in several isolated island populations that have reached carrying capacity, a considerable fraction of the reproductively mature birds ('surplus' birds) is constrained from breeding (e.g.,

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Komdeur 1996a; Holt & Martin 1997; Grant et al. 2000; Kokko & Lundberg 2001) and may never produce offspring over their life time (Komdeur 1992). Mature individuals delaying independent breeding may instead provide care to young that are not their own genetic offspring. The most common form of cooperative breeding involves a breeding pair being assisted by offspring from previous broods. Evolutionary theory is based on the concept that individuals are selected on their ability to efficiently translate resources into reproductive success, thereby maximizing their genetic contribution to future generations (Hamilton 1964; Maynard Smith 1964). As such helpers can increase their inclusive fitness by gaining either indirect fitness benefits from enhancing the reproductive success of close relatives, or direct benefits from increased opportunity for their own future reproduction (e.g. Emlen & Wrege 1989; Mumme et al. 1989; Emlen 1991, 1995; Mumme 1992; Koenig et al. 1992; Cockburn 1998). If helping results in higher fitness than dispersal, individuals should delay dispersal and help. However, in most species the fitness benefit from helping is likely to be considerably less than the potential direct genetic gain from immediate independent breeding if a territory and mate could be obtained (Brown 1987). Thus cooperative breeding can be seen as a 'best-of-a-bad-job' strategy, adopted when opportunities for independent breeding are limited. However, grown offspring may gain inclusive fitness benefits by remaining on the natal territory. To test the fitness benefits of delayed dispersal and helping in the field, detailed knowledge of the fitness functions for males and females is required (Leimar 1996; Lessells 1998; Lessells et al. 1998; Koenig & Walters 1999; Pen & Weissing 2000). These data are not available for most species. In this article I will describe the adaptations and maladaptations to island living in the Seychelles Warbler (*Acrocephalus sechellensis*).

The Seychelles Warbler is a rare island endemic, which from 1920 to 1988 occurred only on Cousin Island (29 ha) in the Seychelles (Fig. 1a). I will describe the fitness consequences of cooperative breeding for the helpers and for their parents, and address some adaptations employed by helpers and parents to enhance their fitness. The Seychelles Warbler is an excellent model species to test the fitness benefits of helping and dispersal behaviour, because of: (i) the ability to measure local dispersal in detail (Komdeur 1992, 2003), (ii) the availability of molecular markers to assess sex, parentage, and coefficients of related-

ness between individuals in the breeding group (Richardson et al. 2000, 2001), and (iii) the wealth of long-term data allowing accurate fitness measures for each individual (Komdeur 2003).

MATERIALS AND METHODS

1) Study populations and data collection

The Seychelles Warbler is a small (15–16 gram) insectivorous bird (Fig. 1b). It is a rare island endemic, which occurred on several islands in the Seychelles (Oustalet 1878; Diamond 1980) until anthropogenic disturbance in the 20th century reduced them to just one population on Cousin Island (Fig. 1a; Collier & Stuart 1985) where by 1967 only ca. 30 individuals remained (Crook 1960; Lousteau-Lalanne 1968). Because the warbler was threatened with extinction, Cousin was purchased in 1968 for Bird Life International with the express aim of saving the warbler. The native vegetation was allowed to regenerate resulting in the warbler population growing to its carrying capacity of 320 birds by 1982. The increase in number of territories showed the same trend and reached its saturation level of ca. 115 territories in 1981 (Fig. 1c). The island was completely covered by territorial groups with no empty spaces (Fig. 1d). Although warblers can breed independently in their first year, some individuals remain in their natal territories as subordinates, and often assist the breeding pair providing nourishment to offspring (Fig. 1b). Habitat saturation has led to cooperative breeding in this species (Komdeur 1992). Once paired, warblers reside permanently in the same territories, sometimes for as long as nine years. On Cousin Island the warbler usually has a clutch size of one egg only, and adult birds have high annual survival (81%). In 1988 and 1990 respectively, new populations of Seychelles Warblers were established by moving 29 birds to both Aride Island (9 km from Cousin) and to Cousine Island (1.6 km from Cousin) (Fig. 1a). These translocations were highly successful, with the founder populations expanding to a combined population of ca. 1,750 individuals by 1996 (Komdeur 2003).

The Cousin Island population of Seychelles Warblers (ca. 320 birds) has been intensively studied since 1985, while the populations on the islands of Aride and Cousine have been studied from establishment. Since 1985 nearly all birds on Cousin Island have been banded for individual recognition and, since 1993, blood sampled for molecular sex and parentage analyses. Off-island migration by warblers

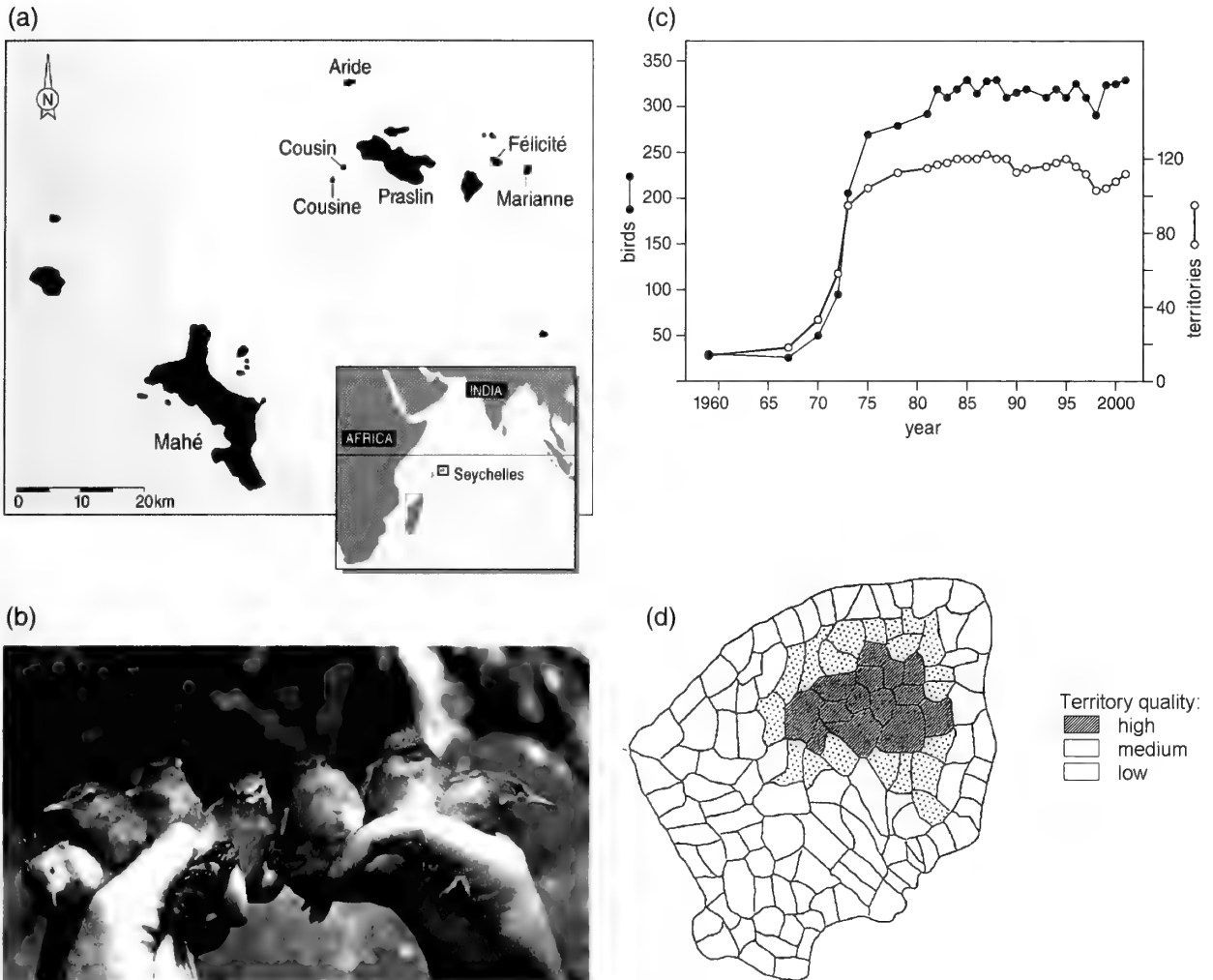


Fig. 1. (a) Map showing the Seychelles islands. Populations of Seychelles Warblers on Cousin, Aride as place of first transfer (September 1988), and Cousine as place of second transfer (June 1990). (b) A complete breeding group of Seychelles Warblers on high-quality territory: a breeding pair, three helpers and their offspring (twins) (from left to right: male (1 year, twin), mother (7 years), female helper (4 years), female helper (2 years), female (1 year, twin) father (6 years) and female helper (2 years); photograph: DS Richardson). (c) Increase in Seychelles Warbler numbers and territories on Cousin Island since 1959. (d) Map of Cousin Island with Seychelles Warbler territories divided into three quality categories: low-, medium- and high-quality territory (from Komdeur 1992).

is negligible (0.10%; Komdeur et al. in press), so birds that have disappeared are considered dead. Each year (1985–2002) nearly all breeding attempts were monitored and activity by resident birds observed during the nest building, incubation and nestling periods (Komdeur 1996b; Richardson et al. 2002). Observations on incubation and food provisioning were made at all breeding attempts to determine the status of the birds within each territory. The primary male and female were defined as the dominant, pair-bonded male and female in the territory, while the term ‘subordinate included all other birds

(> eight months old) resident in the territory. Subordinates were split into three categories: non-helpers, subordinate helpers (non-parents) and subordinate parents. Playing recorded songs at different locations to provoke territory defence behaviour by the focal birds identified territory boundaries. Territory size was assessed using a compass and aerial photographs. Because the warblers are insectivorous, territory quality was expressed in terms of insect prey availability (Komdeur 1992) a factor that has been assessed on a monthly basis within each breeding season. Territories were classified into three territory-

quality categories—low, medium or high (Komdeur 1992).

2) Molecular analyses

The sex of each individual within the study populations was determined using a PCR based method (Griffiths et al. 1998). Genotypes were identified for individuals in the Cousin population using 14 microsatellite markers (Richardson et al. 2000). Coefficients of relatedness between individuals were determined using KINSHIP (Goodnight & Queller 1999) and used to determine, in terms of genetic equivalents, the exact direct and indirect benefits gained by the subordinates (Richardson et al. 2002). Using CERVUS (Marshall et al. 1998) parentage was assigned with high confidence (> 90%) to all offspring sampled between 1997–2000 (Richardson et al. 2001).

RESULTS AND DISCUSSION

1) Benefits of helping to subordinates: difference between the sexes

Indirect fitness benefits have been suggested to be a major selective force behind the evolution of cooperative breeding (Emlen & Wrege 1989; Mumme et al. 1989; Mumme 1992; Koenig et al. 1992, Emlen 1997). These benefits accrue if helping obeys two requirements. First, helping should result in improved survival and reproductive success of the breeding pair. Second, subordinates should preferentially help more closely related kin. In the Seychelles Warbler, removal experiments showed that on high-quality territories the helping behaviour of subordinates increased the reproductive success of the breeding pair (Komdeur 1994a). Furthermore, subordinates were both more likely to become helpers, and provided more help when they were more closely related to the recipient (Komdeur 1994b). However, in this study relatedness was estimated from pedigree data, which was shown to be inadequate when, a decade later, using microsatellite based genotyping we found that complex patterns of shared reproduction and/or extra-group paternity occur in the Seychelles Warbler (Richardson et al. 2001, 2002). Furthermore, it was found that females always become subordinates on their natal territory ($N=43$), whereas a significant percentage of males (25%, $N=20$) became subordinates on non-natal territories ($\chi^2=8.51$, $P<0.05$; Richardson et al. 2002), suggesting that the indirect benefits of helping are more important for females

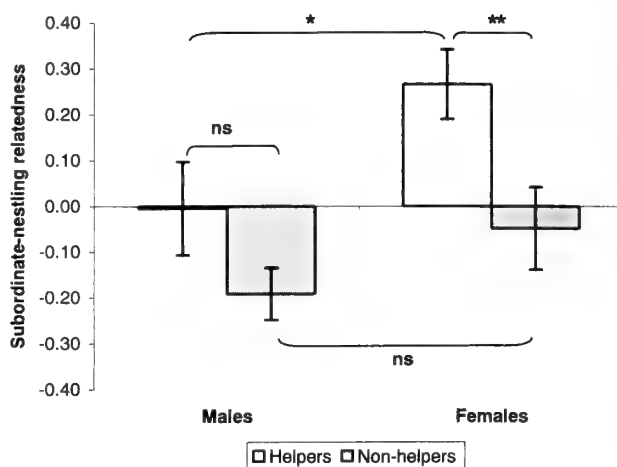


Fig. 2. The relatedness (r) of female and male subordinates to helped or non-helped nestlings. Bars indicate means \pm SE. * $P<0.05$, ** $P<0.01$ (from Richardson et al. 2003a,b).

than for males. Using microsatellite markers to calculate precisely coefficients of genetic relatedness between individuals (see Richardson et al. 2000), we found that female subordinates without parentage accurately maximised their indirect benefits by preferentially feeding more related offspring, produced by relatives of the female subordinate (Fig. 2; Richardson et al. 2003a,b). On the other hand, the amount of help provided by male subordinates was low and independent of relatedness to offspring (Fig. 2; Richardson et al. 2003b).

In the Seychelles Warbler unrelated subordinates (born in other groups) do sometimes help (DS Richardson, pers. comm.) suggesting that direct benefits, such as improved parental skills or gaining parentage (Koenig et al. 1992; Cockburn 1998), or territory inheritance (Emlen 1991; Koenig et al. 1992; Balshine-Earn et al. 1998) are important too. To test whether helping improved the reproductive success of subordinates that later become breeders, we translocated male and female warblers of the same age but with different degrees of previous breeding experience, to the islands of Aride and Cousine. Individuals were categorised as: (i) experienced breeders that had fledged young of their own in a previous year; (ii) experienced subordinates with no breeding experience but with helping experience; and (iii) inexperienced birds that had neither helping nor breeding experience (see Komdeur 1996b). On the new islands birds with helping experience that were paired with an experienced partner produced their first fledgling as fast as experienced breeders, and significantly faster than inexperienced birds paired

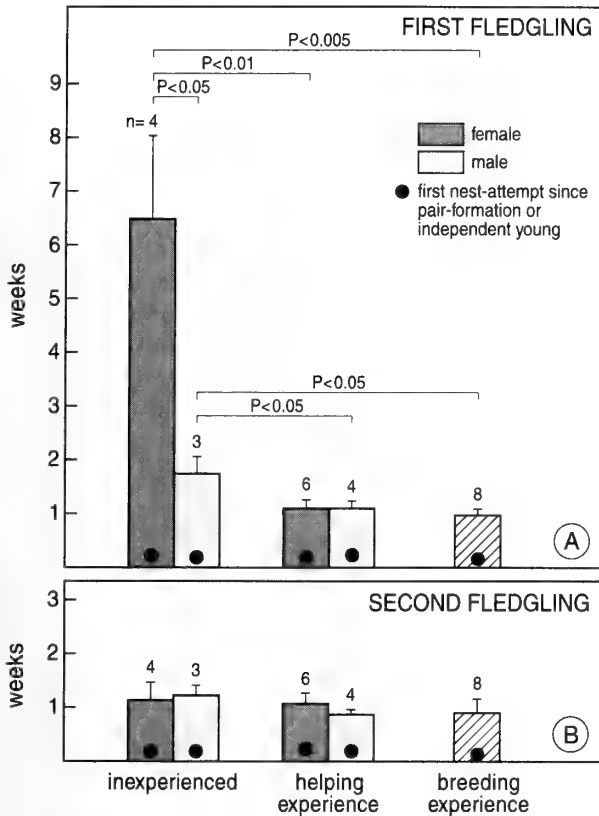


Fig. 3. (A) The number of weeks between pair formation and the production of the first nest and first fledgling on the islands of Aride and Cousine plotted for male and female birds with different past experience. (B) The number of weeks between independence of first fledgling and the production of a new nest and second fledgling on the islands of Aride and Cousine plotted for the same male and female birds as in (A), who have become experienced breeders. In both figures, the birds were between 3 and 7 years of age (i.e., the period during which there are no age effects on reproduction), paired with the same experienced breeding partner, and did not receive assistance from helpers. Statistically significant comparisons determined by Mann-Whitney U tests. Only significant differences are plotted. Error bars represent one standard error (from Komdeur 1996b).

with an experienced partner (Fig. 3; Komdeur 1996b). Females with helping or breeding experience built better nests and spent more time incubating than inexperienced females. During this period no subordinates assisted any of the breeding pairs. Pairs comprising a male with breeding experience and an inexperienced female, took four times longer to produce their first fledgling than pairs consisting of a female with breeding experience and an inexperienced male (Fig. 3). This is probably because only females build nests and incubate the clutch. Once inexperienced birds had fledged young and had, therefore, acquired

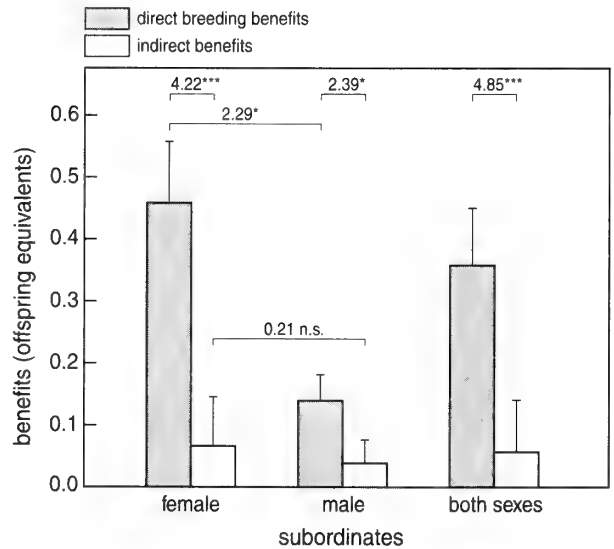


Fig. 4. The fitness benefits of cooperative breeding gained by female and male subordinates in the Seychelles Warbler (1997–1999). Statistical significance assessed by Mann-Whitney Z statistic. Both female ($N=43$) and male ($N=20$) subordinates gain significantly higher direct breeding benefits (open columns) compared to indirect benefits (filled columns). Direct breeding benefits are significantly higher in females than in males, but there is no significant difference between the sexes in indirect breeding benefits. Error bars represent one standard error (from Richardson et al. 2002).

breeding experience, they subsequently improved their breeding success by producing a second fledgling in the same time interval as birds with either helping or breeding experience (Fig. 3).

Another direct benefit gained by subordinate Seychelles Warblers is the acquisition of parentage within the breeding group by sneaking their own eggs into their mother's nest (44% of 43 female subordinates; Richardson et al. 2001, 2002). Subordinate males gained significantly less often parentage within the group (15% of 20 male subordinates) than females (Fisher's exact test, $P=0.024$; Richardson et al. 2002). None of the subordinate females gained reproductive success through egg dumping in other territories and none of the male subordinates gained extra-pair fertilisations with females from other groups. Overall direct benefits were significantly higher than indirect benefits, although this difference was more extreme in females (Fig. 4; Richardson et al. 2002). These results show that females remaining on the natal territory as helpers gain greater benefits than male helpers and this may explain why most helpers are female (percentage subordinates that are female: 88% (Komdeur 1996c) and 68% (Richardson et al.

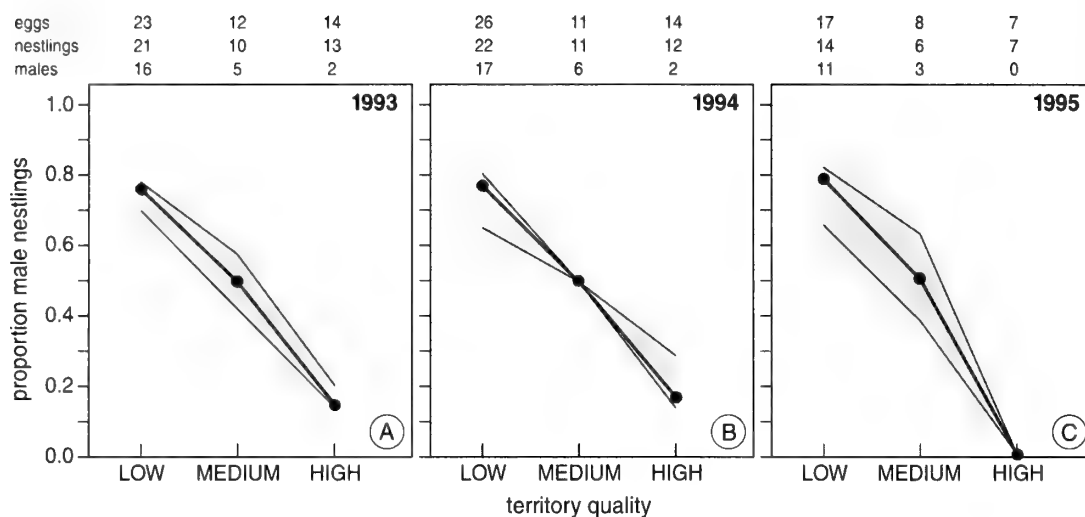


Fig. 5. Sex ratio of nestlings produced by Seychelles Warbler pairs in relation to quality class of breeding territory (tq classes: low-quality territory, medium-quality territory; and high-quality territory; 1993–1995). No additional young were present on the territory. Young were hatched from one-egg clutches only in different years (A, 1993: $N=46$, G-test of independence: $D=12.23$, $df=1$, $P=0.0005$, proportion male $=1/(1+e^{-z})$, $z=-2.68+1.36$ (tq class); B, 1994: $N=45$, $D=12.03$, $df=1$, $P=0.0005$, $z=22.68+1.37$ (tq class); C, 1995: $N=27$, $D=12.99$, $df=1$, $P=0.0003$, $z=-3.60+2.10$ (tq class)). Shaded area represents the maximal and minimal values for the sex ratio assuming that all unhatched eggs were male, or females, respectively (from Komdeur et al. 1997)

2002)).

2) Adaptive manipulation of egg's sex

Given that helpers on high-quality territories increase their parents' reproductive success (Komdeur 1994a), it may be that primary birds on high-quality territories preferentially accept or produce female subordinates to increase their fitness. On the other hand, given that helpers on low-quality territories reduce their parents' reproductive success (Komdeur 1994a) females on low-quality territories may preferentially produce males, which disperse in order to avoid having future helpers. Helpers are mostly females, and females (in birds females determine the sex of an offspring because they are the heterogametic (ZW) sex) may adjust the sex of their single egg to territory quality (Komdeur 1996c). Reviews from the 1980s were unanimous in the belief that facultative adjustments of offspring sex ratio at birth were unlikely to occur in vertebrates (Williams 1979; Charnov 1982; Clutton-Brock 1986; Bull & Charnov 1988). Sex determination is almost ubiquitously associated with chromosome heterogamety, constraining the physiological or genetic mechanisms for skewing the sex ratio at birth (Williams 1979, 1992; Krackow 1995). The occurrence of adaptive sex ratio manipulation at laying in birds has, therefore, been questioned. At the time we were able to demonstrate that

Seychelles Warblers adaptively modify the sex of their single egg. The fraction of male eggs produced by unassisted Seychelles Warbler mothers changed significantly with territory quality (Fig. 5; Komdeur 1996c; Komdeur et al. 1997). Unassisted females on high-quality territories produced 88% female eggs ($N=32$), whereas unassisted females on low-quality territories produced 77% males eggs ($N=57$), the dispersing sex (Komdeur et al. 1997). This was confirmed by experiments: (i) Helper removal experiments confirmed that sex ratio bias was for the purpose of producing helpers. When females on high-quality territories had their female helpers experimentally removed they switched from producing all sons to producing 83% females (Komdeur et al. 1997). (ii) Breeding pairs that were transferred from low- to high-quality territories switched from the production of male to female eggs (Komdeur et al. 1997). In the short term, the manipulation of the offspring's sex is directly adaptive from the perspective of the breeding pair. The next step is to determine whether egg sex-ratio manipulation results in long-term inclusive fitness benefits for the breeding pair.

3) Inter-island dispersal

The co-operative breeding and sex-allocation system of the Seychelles Warbler is a beautiful example of behavioural and life history adaptations to re-

stricted circumstances. However, a paradox still remains. Genetic parentage analysis has demonstrated that a substantial proportion of adult female and male birds died without having produced offspring of their own (12%; D.S. Richardson, unpublished data). These warblers would have done better if they had colonised the suitable islands of Aride and Cousine by themselves, where initially the annual production of yearlings by breeding pairs that were artificially translocated to Aride and Cousine was, on average, 14 times higher than before the translocation (Komdeur 1996d). These islands have been suitable for Seychelles Warblers for at least 25 years. Despite the saturated nature of the Cousin Island population and the possibility of obtaining higher reproductive success on new islands (Komdeur 1996d), inter-island dispersal by Seychelles Warblers is extremely rare. During the 20 years of study only two warblers (0.10%, $N=1,924$) have been observed to fly between these islands (Komdeur et al. in press). Energy conservation is proposed to be the selection pressure behind reduced flight ability and, compared to closely related flying species, flightless birds usually have smaller pectoral muscles, relative to body mass, wing shape and wing loading (Livezey 1990; 1992a,b; McNab 1994b; McCall et al. 1998). The Seychelles Warbler does not fit the predictions of the energy conservation theory, as neither the average pectoral mass relative to body mass, the skeletal attachment area, the wing shape nor the wing loading is distinct from those of its migratory relatives (Komdeur et al. in press). Seychelles Warblers show the morphological structures required for sustained flight, but still do not manage to disperse successfully to relatively close suitable islands. Seychelles Warblers appear, therefore, to have a behavioural reluctance to cross what they may regard as extensive bodies of water. This phenomenon of 'psychological flightlessness' occurs in other species that are capable of sustained flight (Diamond 1981, Raikow 1985). Given the historical presence of discrete island populations of Seychelles Warbler and the vulnerability to extinction of such populations, we would not expect the Seychelles Warblers to have lost the ability or willingness to disperse across water to colonise new islands. The anatomical and behavioural bases of dispersal are subject to natural selection (Diamond 1981). Therefore, one would expect that the ability to disperse over water, and settle on nearby suitable islands (where, as shown by the translocations, individuals could gain higher fitness) should have been main-

tained in this species. The reluctance to do so could have developed a long time ago when, perhaps, all Seychelles islands were fully occupied by warblers. Under these conditions, dispersal over water was not an adaptive strategy as all islands may have been saturated with warblers. Perhaps it is only now, after 100 years in which warblers have disappeared from all but one island, that flying across water to breed on other islands would be adaptive. The case of the Seychelles Warbler may exemplify the inability of natural selection to plan ahead!

CONCLUDING REMARKS

The Seychelles Warbler is atypical in cooperative breeding birds in that females are more likely than males to become subordinates. Males typically disperse. Our results show that female subordinates gain significantly higher inclusive fitness benefits than male subordinates. Female subordinates remain on their natal territory and obtain higher inclusive reproductive success by helping closely related relatives, by co-breeding within the group, and through improved future parenting ability. Males often become subordinates on non-natal territories and so do not gain indirect reproductive success by helping. The higher inclusive fitness benefits accruing to female subordinates may explain why primary females often skew the sex ratio towards producing female offspring (Komdeur et al. 1997). With female subordinates remaining on the natal territory the primary female gains both an increase in her own productivity and also indirect benefits associated with subordinate females breeding. The presence of several female subordinates in the group may, however, be a disadvantage to the primary female, because her direct fitness declines due to competition for food and increased nest failure (mainly egg breakage due to increased pressure from simultaneous incubation; Komdeur 1994b). Her indirect fitness may also decline because of increased competition over local breeding vacancies between subordinate female relatives. At this stage female offspring should refrain from becoming subordinates and disperse. The balance between these forces should determine whether offspring become subordinates or not.

There is good evidence that the inclusive fitness consequences are higher for female subordinates than for male subordinates in the Seychelles Warbler. However, the long-term inclusive fitness functions for subordinates and non-subordinates of both sexes

should be calculated using molecular parentage analyses and precise coefficients of genetic relatedness, in order to predict under which circumstances males and females should become subordinates.

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INVITED ARTICLE

Translocations in avian conservation: reintroduction biology of the South Island Saddleback (*Philesturnus carunculatus carunculatus*)

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Abstract Translocation is a commonly used tool in conservation management. However, because post-release monitoring has been infrequent in the past, reasons for the outcomes of translocations have often been unknown. Here, I review the reintroduction biology (including dispersal patterns, social organisation, survival, habitat use and foraging patterns) of a population of 26 South Island Saddlebacks (*Philesturnus carunculatus carunculatus*), on Motuara Island, New Zealand. After release on Motuara Island, South Island Saddlebacks dispersed widely through forest areas. During their first post-release breeding season, saddlebacks established territories of 1.9 ha–8.8 ha (\bar{X} =4.21 ha, SD=2.42) in size, and territorial confrontations were very rare. Saddlebacks bearing both adult and subadult plumage held territories and attempted to breed, and successful breeding produced approximately 10 fledglings. Saddlebacks foraged on a variety of plant species, dead wood and the ground. Except for five-finger (*Pseudopanax arboreus*), a preferred foraging substrate, birds foraged in all plant material in proportion to its availability. Saddlebacks preferred to forage in the lower levels of the forest. Although vegetation composition differed significantly between territories, all territories contained forest areas, and birds appeared to prefer foraging in larger sized trees. Large territory sizes, breeding attempts by young birds and rarity of territorial confrontations are most likely products of low population density. As density increases, birds are expected to occupy smaller territories, forage more efficiently within these smaller areas, start breeding at older ages, and possibly colonise scrub habitats. The translocated group sustained no more than 50% mortality at 8–10 months after release. In the past, translocations of 15–59 South Island Saddlebacks have been successful, suggesting that the relatively small founder group does not threaten the success of the transfer to Motuara Island. Saddlebacks are flexible in their habitat use, appear to readily adapt to ‘new’ environments and have high reproductive potential, increasing the likelihood of success of translocations of this species.

Key words New Zealand, *Philesturnus carunculatus carunculatus*, Reintroduction, South Island Saddleback, Translocation

Translocation is becoming increasingly commonly used for conservation, and can be defined as the intentional release of plants or animals to the wild to establish, re-establish or augment a population (IUCN 1987; Griffith et al. 1989). The technique has been applied to the conservation of mammals (e.g. Duffy et al. 1994; Short et al. 1994), invertebrates (e.g. Sherley 1994) and birds (e.g. Atkinson & Bell

1973; Merton 1973, 1975; Bell 1978; Butler & Merton 1992). In New Zealand, translocations have often been incorporated into species management programs in the past, and have been successful in saving some New Zealand birds from extinction. Since the 1880s, almost 400 translocations of 50 taxa (42 birds, five reptiles and three invertebrates) have been conducted in New Zealand, often in emergency situations, such as in 1962 when ship rats (*Rattus rattus*) arrived at the last stronghold of the South Island Saddleback (*Philesturnus carunculatus carunculatus*) (Atkinson & Bell 1973; Merton 1973, 1975; Bell 1978).

Despite the increasingly common application of

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translocations in conservation management, and wide recognition of the value of post-release monitoring (e.g. Scott & Carpenter 1987; Griffith et al. 1989; Sarrazin & Barbault 1996), such monitoring does not always occur. In fact, Wolf et al. (1996) reported that only 45% of 336 bird and mammal translocation programs included tagging of released individuals or post-release telemetry, and in about 30% of translocations, the causes of 90–100% of animal losses were never identified. In New Zealand, translocation continues to be widely used as a conservation tool. Post-release monitoring of translocated animals may be becoming more common (e.g. Nelson et al. 2002), but such monitoring seldom occurred in the past (Department of Conservation 1994; Lovegrove & Veitch 1994; Armstrong & McLean 1995).

Similar to post-release monitoring of survival, monitoring the habitat use of newly translocated organisms is important, yet seldom occurs. Globally, translocations are deemed most likely to succeed where animals are released into areas of high habitat quality and/or quantity (Wolf et al. 1996). This emphasizes the importance of thoroughly investigating the habitats at potential release sites before conducting translocations and monitoring the habitat use of translocated animals after they are released. Post-release monitoring of habitat use can confirm suitability of the new location, and produce valuable information relevant to future translocations, thereby facilitating adaptive wildlife management (Sarrazin & Barbault 1996). For example, mobile animals at low densities may occupy habitats on the basis of preference rather than requirement, and may colonise less 'preferred' areas as their population density increases (Jenkins 1976; Armstrong & McLean 1995). Therefore, monitoring spatiotemporal patterns of habitat use together with population growth can be informative in determining habitat requirements and preferences, and the ability of translocated organisms to colonise 'novel' environments.

The South Island Saddleback is a forest passerine endemic to the islands of New Zealand. It is an endangered subspecies of the near threatened New Zealand Saddleback (IUCN 2000). Diurnal, territorial and largely insectivorous, the South Island Saddleback forages on foliage, live and dead wood, and the ground. It uses cavities for roosting and is monogamous with apparently flexible nest site requirements (Guthrie-Smith 1925; Pierre 1995). Although the South Island Saddleback was formerly widespread over New Zealand's South Island and southern off-

shore islands, it is unable to coexist with introduced predators, and consequently, was virtually extinct by 1900 (Oliver 1955; Roberts 1991). The total population of South Island Saddlebacks is currently about 650, with birds occurring on 11 islands, all of which are free of introduced predators.

Following the South Island Saddleback Recovery Plan (Roberts 1991) administered by the New Zealand Department of Conservation, 26 South Island Saddlebacks were translocated to Motuara Island in the Marlborough Sounds from the Titi Islands near Stewart Island, New Zealand, in March 1994. (See Figure 1 for the locations of islands mentioned in the text). Seven adult males, 11 adult females, 5 subadult males, one subadult female and one adult and subadult of unknown sex were included in the translocated founder population. Motuara Island (59 ha) was selected as the release site for translocated South Island Saddlebacks for three main reasons. First, introduced predators (*Rattus exulans*) were extirpated from the island in 1993. Second, vegetation on Motuara Island has been regenerating since farming was abandoned in 1926 (W.F. Cash pers. comm.), and finally, the bird was historically resident in the area. Conservation managers considered Motuara Island to be sufficiently large and with appropriate

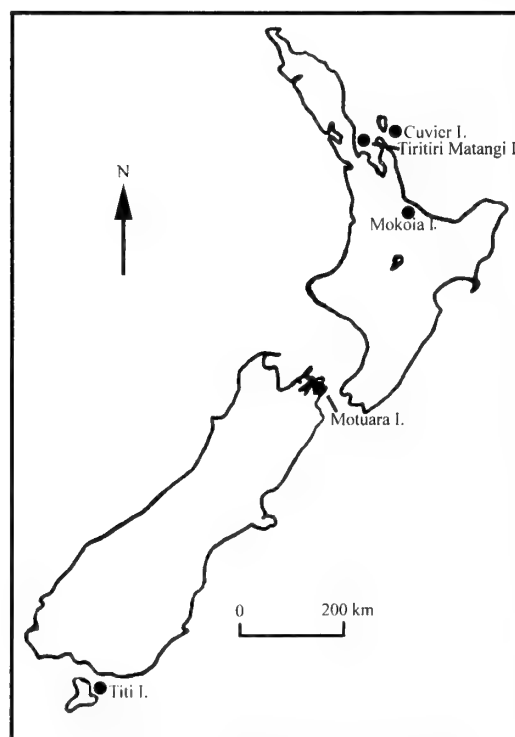


Fig. 1. Locations of islands mentioned in the text. (From Pierre 1999).

habitat to support more South Island Saddlebacks than currently existed on any other island (W.F. Cash pers. comm.).

In this paper, I review the reintroduction biology of the South Island Saddleback. I discuss post-release dispersal, social organisation, survival, habitat use and foraging patterns of the newly released population on Motuara Island, New Zealand. Before the work described in this review was carried out, the South Island Saddleback had not been studied in detail. Also, future translocations were planned to increase the total population of this bird (Roberts 1991). For these reasons, post-release monitoring of the translocated population was critical.

METHODS

Saddlebacks were weighed, measured and their plumage examined on capture to determine sex and age (W.F. Cash pers. comm.; Nillson 1978; Jenkins & Veitch 1991). Numbered metal and unique combinations of coloured plastic legbands were used to identify individuals. After release on Motuara Island, birds were relocated using a recording of South Island Saddleback male territorial song, and via their vocal responses and attraction to disturbances (e.g. logs breaking). The work reviewed here results from post-release monitoring involving intensively searching for birds for four days, six months after they were released, and searching for and monitoring birds for 56 days, from eight months after release, during their first breeding season on Motuara Island.

Territory boundaries were identified during the breeding season by conducting repeated searches for birds and recording the locations of song posts. I monitored birds for 90 minutes during these tracking episodes; tracking beyond five 90 minute sessions did not alter the perceived location of territory boundaries (Pierre 1999). As well as recording song posts, I monitored habitat use by birds, including substrates used for foraging and other activities, and heights of the forest that birds occupied (Pierre 2001). I also recorded prey identity when possible, and where prey were caught (Pierre 2000). Saddleback nests were located by following birds holding nesting materials, and by checking nest boxes. To avoid disturbing nesting birds, I did not check nests frequently after locating them. Instead, I monitored breeding activities indirectly by assessing the behaviour of adult birds (Pierre 1999).

I conducted analyses of habitat use and foraging

data using paired *t* tests and analysis of variance (ANOVA) conducted in SPSS 8.0 (SPSS Inc. 1997). I used Games-Howell post-hoc tests (Day & Quinn 1989) to identify homogeneous subgroups after significant ANOVAs, and Bonferroni α adjustments when appropriate, including in *G* tests described below (Miller 1981). See Pierre (2001) for a discussion of how pseudoreplication and problems of independence were minimized.

I characterised vegetation using a transect-quadrat sampling method, and sampled both saddleback territories and one area uninhabited by saddlebacks (Pierre 2001). I defined plant availability as the cross-sectional area of each plant species at breast height, and the availability of dead wood as the proportion of total quadrat area it covered on each transect (Pierre 2001). Vegetation characteristics were compared between sites using *G* tests (Zar 1996).

RESULTS

After release, South Island Saddlebacks ranged widely through the forested areas of Motuara Island. By the start of the first post-release breeding season, both adult and subadult birds appeared to have settled on territories, which varied in size from 1.9–8.8 ha (\bar{X} = 4.21 ha, SD = 2.42, N = 6, Figure 2, Pierre 1999). Adult and subadult saddlebacks announced their presence vocally from a range of vertical locations in their territories, especially in the first two hours after dawn, and for approximately one hour just before dusk. However, confrontations between neighbours appeared very rare, and I observed only one during the study. This low frequency was despite saddlebacks venturing into each other's territories, which I observed on five occasions during my research, and which at least sometimes appeared related to searches for water (Pierre 1999).

The vegetation composition of saddleback territories on Motuara Island differed significantly, and was different again in areas uninhabited by saddlebacks (*G* tests, vegetation composition in all territories compared to all other territories and a vegetated area not occupied by saddlebacks: $G_8 > 2117.36$, $P < 0.005$, Pierre 2001). However, all territories were in forest areas and included plants of similar size distributions (*G* tests: plant sizes in all territories compared to all other territories, $G_5 \leq 14$, $P > 0.005$, NS). In contrast, saddlebacks did not inhabit a locality covered by smaller diameter plants, in this case scrub (*G* tests: all territories compared to an area uninhabited by saddle-

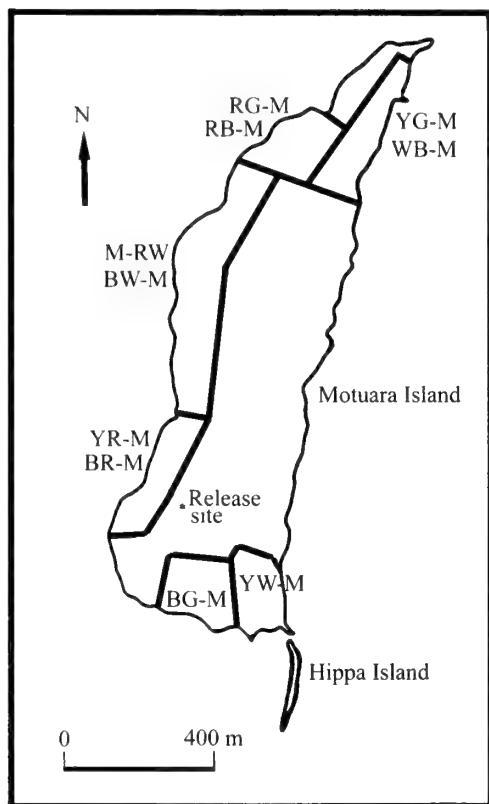


Fig. 2. South Island Saddleback territory boundaries during 11 Nov 94–13 Jan 95, the first breeding season after release. Letters denote legband combinations: B=blue, G=green, M=metal, R=red, W=white, Y=yellow. (From Pierre 1999).

backs, all $G_5 \geq 26$, $P < 0.005$, Pierre 2001).

At least five, and possibly six pairs of saddlebacks were present during the first post-release breeding season on Motuara Island. Pairs were not knowingly transferred together, and after release at least some birds interacted with more than one potential mate before settling on a territory with what appeared to be a stable partner (Pierre 1999). Both adult birds and those in subadult plumage formed pairs and attempted breeding during the first post-release breeding season. Pairs were able to form and then initiate breeding with what appeared to be minimal delay; one pair built a nest and reared two offspring no more than 35 days after pairing. This pair then appeared to reneest (Pierre 1999). The nests of two other pairs were found in a tree hole and a nest box, and held one and two eggs, respectively. However, these nests were deserted for unknown reasons. In all, an estimated 10 fledglings were hatched the first breeding season after saddlebacks were released onto Motuara Island (Pierre 1999; W.F. Cash pers. comm.).

Translocated saddlebacks utilised a range of foraging substrates, including various plant species, dead wood and the ground. Foraging patterns differed between males and females, with males spending the most foraging time on the ground, whereas females preferred to forage in five-finger (*Pseudopanax arboreus*) (ANOVA: $F_{5,29} = 4.59$, $P = 0.003$, Figure 3, Pierre 2001). Overall, birds apportioned their foraging time differently among different foraging substrates, and spent the most time foraging on the

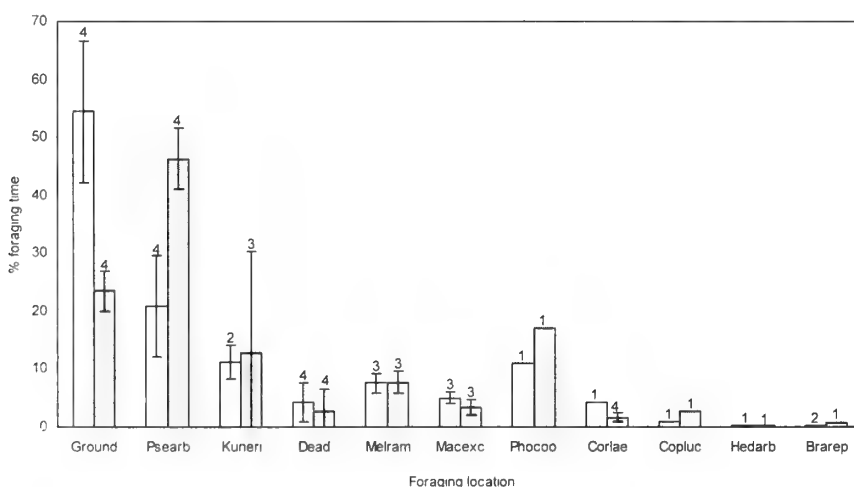


Fig. 3. Percent time spent on foraging sites ($\bar{X} \pm 1$ SE) by male (open bars) and female (hatched bars) South Island Saddlebacks on Motuara Island. Brarep=*Brachyglottis repanda*, Copluc=*Coprosma lucida*, Corlae=*Corynocarpus laevigatus*, Dead=dead wood, Hedarb=*Hedycarya arborea*, Kuneri=*Kunzea ericoides*, Macexc=*Macropiper excelsum*, Melram=*Melicytus ramifloris*, Phocoo=*Phormium cookianum*, Psearb=*Pseudopanax arboreus*. Numbers above bars represent the number of birds contributing to means. (From Pierre 2001).

ground and five-finger (ANOVA: $F_{5,29}=13.08$, $P<0.001$, Figure 3, Pierre 2001). However, birds used most plant species (and dead wood) in proportion to their availability (t tests: $t_{1-6}=-1.14-2.87$, $P=0.21-0.99$), except for five-finger (used more than expected, t test: $t_6=2.74$, $P=0.03$). Flax (*Phormium cookianum*) may also have been used more than expected, although small sample size rendered this impossible to test statistically (Pierre 2001). The number of prey items South Island Saddlebacks obtained from foraging substrates was roughly in proportion to the amount of foraging time spent, although dead wood was a particularly rich foraging substrate. Saddlebacks were largely insectivorous, but also fed on nectar and honeydew (Pierre 2000).

Saddlebacks were recorded significantly more frequently in the lowest two metres of the forest than at any other level (ANOVA: $F_{4,30}=41.31$, $P<0.001$, Pierre 2001). This was the case for both males and females, whose vertical use of the forest did not appear to differ (ANOVA: $F_{4,30}=0.20$, $P=0.94$, however $1-\beta=0.16$ at $\alpha=0.1$, Pierre 2001).

Saddlebacks were observed drinking water frequently, both from natural sources and troughs constructed on the island before birds were released. They also bathed in these human-made water troughs frequently (Pierre 2001).

Mortality of South Island Saddlebacks was 35% (9/26 birds dead) at six months after release. Maximum mortality was 50% 8–10 months after release. Of the surviving 13/26 translocated saddlebacks, there were 3/7 adult males, 4/11 adult females and 6/7 subadults remaining (Pierre 1999).

DISCUSSION

After release on Motuara Island, South Island Saddlebacks traversed forested areas widely, before settling on territories after about eight months. Translocations of North Island Saddlebacks (*P. c. rufusater*) also result in wide post-release dispersal, suggesting that this is the norm for the species (Jenkins 1976; Armstrong & Craig 1995). South Island Saddlebacks settled on territories that were unusually large and variable in size. There is little data on territory size in saddlebacks, but on Cuvier Island (170 ha), two pairs of North Island Saddlebacks held territories of 0.89 ha and 1.22 ha in November/December, the height of the breeding season. The smallest territory on Motuara Island was about 1.5–2 times this size, suggesting that the low density of saddlebacks on Motuara Is-

land had strong effects on the area of territories. The size of North Island Saddleback territories has been recorded to change temporally, with territories being largest during breeding (O'Callaghan 1980).

South Island Saddlebacks on Motuara Island were much less vocal than North Island Saddlebacks occurring in higher density populations. However, temporal singing patterns appear similar for both subspecies (pers. obs.; Jenkins 1976; Murphy 1989). Territorial confrontations occurred rarely on Motuara Island, relative to North Island Saddleback populations (Jenkins 1976; O'Callaghan 1980). This is probably because saddleback territories on Motuara Island were sufficiently large that neighbours would seldom meet, and may have been out of earshot of each other often, if not most of the time. The utility and importance of song in maintaining territorial integrity might be expected to increase with increasing population densities, however Murphy (1989) showed that the number of neighbours around North Island Saddleback territories did not affect singing rates. The frequency of territorial displays, however, is known to increase with population densities in North Island Saddlebacks (Jenkins 1976; O'Callaghan 1980).

South Island Saddleback territories on Motuara Island were not areas of completely exclusive use by territory 'owners'. This may not be unusual for the species. In a relatively high density population, O'Callaghan (1980) documented areas of overlap between North Island Saddleback territories, as well as subadults and non-territorial adults moving through the territories of others.

Vegetation composition of all saddleback territories differed on Motuara Island. Further, saddlebacks seemed to prefer areas with larger trees; all territories were at least partially forested, compared to uninhabited areas in which the dominant vegetation type was scrub. The species composition of forest however, did not seem important. Habitat characteristics, e.g. the availability of food, affect the size of North Island Saddleback territories (Blackburn 1964; O'Callaghan 1980). Despite this, South Island Saddleback territories were probably much larger than the area required to support a breeding pair (also see above) and as previously mentioned, the large size is almost certainly a product of low population density.

In low density North Island Saddleback populations, birds also preferentially occupy forest habitat. However, with increasing density, birds will colonise scrub areas, and can breed very successfully in this habitat type (Jenkins 1976; Craig 1994; B. Walter

pers. comm.). Thus, it is expected that as the South Island Saddleback population density increases on Motuara Island, birds will colonise scrub areas. On Tiritiri Matangi Island, the suitability of scrub may have been increased by the erection of roost and nest boxes (B. Walter pers. comm.). Thus, the addition of roost and nest boxes may enhance the suitability of scrub areas for saddlebacks on Motuara Island. In any case, the colonisation of scrub demonstrates the behavioural plasticity of saddlebacks. Both for saddlebacks and other organisms, behavioural plasticity can be an important factor increasing the success of translocations.

After release on Motuara Island, but before settling on a territory in a stable pair, some South Island Saddlebacks were observed with more than one bird of the opposite sex. This has also been reported in newly translocated North Island Saddleback populations (Armstrong & Craig 1995). Further, pairs of North Island Saddlebacks translocated together did not maintain their pair bond after release (Armstrong & Craig 1995). Also, similar to my results for South Island Saddlebacks, North Island Saddlebacks in low density populations are recorded breeding at one year old (Craig 1994). However, in high density populations, North Island Saddlebacks breed at two or more years of age (Lovegrove 1980). Further, South Island Saddlebacks were able to breed successfully with one pair taking a maximum of only 35 days between pairing and nest building. This pair fledged two chicks and probably re-nested in the first breeding season after translocation. Although there are no published records of the length of time taken from pairing to nesting, newly released North Island Saddlebacks have also been reported to raise more than one brood per breeding season (Jenkins 1976; Craig 1994; Armstrong & Craig 1995).

Like South Island Saddlebacks on Motuara Island, North Island Saddlebacks appear to be flexible in terms of foraging substrates they can use (Atkinson 1964, 1966; Lovegrove 1980). Male and female South Island Saddlebacks had slightly different foraging strategies in terms of substrate used and vertical location. Similarly, albeit at high density, North Island Saddleback males spent more time foraging on the ground than their female counterparts (Blackburn 1964; Lovegrove 1980; O'Callaghan 1980), however, whether there are intersexual differences in their foraging patterns at low density is unknown. Out of all plant species (including dead wood) that saddlebacks on Motuara Island foraged on, five-finger and possi-

bly flax were used more than expected. Foraging selectivity of high or low density North Island Saddleback populations cannot be compared, due to lack of research. However, I expect that as population density increases, South Island Saddlebacks may use a wider spectrum of plants to increase the efficiency of foraging in smaller territories. Published data reporting relative richness of locations of prey capture are nonexistent for North Island Saddleback populations. However, as saddlebacks appear flexible with respect to foraging strategies and diet, these are expected to vary with habitat type as well as season, as are the importance of different foraging substrates and prey types (Atkinson 1964, 1966; Blackburn 1964, 1967; Lovegrove 1980, 1992; O'Callaghan 1980; Pierre 1995).

South Island Saddlebacks on Motuara Island foraged mostly in lower levels of the forest, like North Island Saddlebacks at high density (Lovegrove 1980; O'Callaghan 1980). However, high density populations of North Island Saddlebacks also display vertical stratification within pairs when foraging (Lovegrove 1980; O'Callaghan 1980). This may function to reduce intersexual competition within pairs, and improve the efficiency of resource use in territories. As increasing population density causes territory sizes to decrease on Motuara Island, birds may develop vertically stratified foraging behaviour. Coincident with this speculation, an increased degree of vertical stratification in North Island Saddleback foraging behaviour has been related to decreases in territory size (Lovegrove 1980).

Although the diet of saddlebacks contains some water, most of Motuara Island is very dry, and birds used both natural and human-constructed water sources frequently. That saddlebacks used water sources outside their own territories suggests a very strong need for water, and as predicted prior to the translocation, the instalment of water troughs may have increased the quality of saddleback habitat on Motuara Island, possibly increasing the likelihood of success of the translocation.

Mortality rate is one of the most important factors determining the size of founder groups, making it a key consideration when planning translocations. On Motuara Island, maximum mortality was 50% 8–10 months after saddlebacks were released. Published records of North Island Saddleback mortality range from 8% at six months to 52% at two years after release (Jenkins 1976; Armstrong & Craig 1995). Naturally, mortality will vary due to site-specific charac-

teristics as well as the ability of birds to deal with the stresses of capture and translocation, and their flexibility in adapting to new environments. Weather conditions after release and the abundance of natural predators are other important considerations.

In general, for a translocation into excellent quality habitat to have a 60% chance of success, the recommended size of the founder group is fifty individuals (Griffith et al. 1989). Only 26 South Island Saddlebacks were released onto Motuara Island, but in the past, translocations of 15–59 South Island Saddlebacks have been successful (Nillson 1978; Roberts 1991). Thus, from the outset, the success of the transfer to Motuara Island may not have been jeopardized by the relatively small founder group. In combination with the predator-free environment of Motuara Island, the saddlebacks' flexible habitat requirements and foraging strategies, ability to readily adapt to 'new' habitats, and potential for high reproductive output increased the likelihood that translocations to this island would be successful.

In the eight years since translocation, estimates of the number of saddlebacks Motuara Island can support have ranged from about 70 (in years of cold, wet climatic conditions, when breeding success is low) to 150–200 (in the first years after release, with high reproductive output, an abundance of prey and favourable climate) (Pierre 1995; W. F. Cash pers. comm.). Social organisation, survival, foraging ecology and diet have not been investigated in detail since my work was completed. However, due to the success of this translocation over the first eight years at least, the Motuara Island population is now being used as a source population for other South Island Saddleback translocations.

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ORIGINAL ARTICLE

Sexing White-rumped Munias in Taiwan, using morphology, DNA and distance calls

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Abstract Methods of sexing the White-rumped Munia *Lonchura striata phaethon-toptila* were investigated in eastern Taiwan. Twenty-six individuals were captured and their physical parameters were measured in the hand. Distance calls emitted when the birds were released were also recorded. The sex of each bird was confirmed using a DNA sexing method in the laboratory. Among the morphological traits measured, the tails and wings of males were significantly longer than those of females. An increasing stepwise discriminant analysis was performed to determine sex on the basis of morphological characters, however, only 84.0% of individuals were sexed correctly by such analysis. Distance calls of the White-rumped Munia were very similar to those of the Bengalese Finch, *Lonchura striata* var. *domestica*, the domesticated strain of the White-rumped Munia. Two distinct distance calls were recorded from birds on release, corresponding to the sexual difference confirmed by DNA testing. It is concluded, therefore, that the difference in distance calls is a useful trait that facilitates separation of the sexes in the field.

Key words CHD gene, Distance call, Morphology, *Lonchura striata phaethon-toptila*, *Lonchura striata* var. *domestica*, Sexing method

Many species of munias (Estrildidae) are sexually monomorphic (Restall 1996), making it impossible to sex in the field. The White-rumped Munia *Lonchura striata* is one such monomorphic estrildid species that is widely distributed in South- and Southeast Asia (Paynter 1968; Restall 1996). Six (Paynter 1968) to eight (Restall 1996) subspecies occur in this region. They inhabit in a wide range of habitats, from open grassland and cultivated land, to human residential area such as urban gardens and parks (Restall 1996).

Although the White-rumped Munia is a common bird in Asia, little fieldwork has been done on this species (but see Avery 1978, 1980a, b; Chattopadhyay 1980; Young 1989). The Bengalese Finch, *Lonchura striata* var. *domestica*, is a domesticated

strain of the White-rumped Munia (Restall 1996; Honda & Okanoya 1999), and during the process of domestication, several modifications in coloration and behavior have occurred. In particular, males of the Bengalese Finch sing more complex songs than those of wild White-rumped Munias (Honda & Okanoya 1999). The Bengalese Finch has been described as having sexually dimorphic distance calls (Yoneda & Okanoya 1991; Okanoya & Kimura 1993), as has the White-rumped Munia (Restall 1996). Okanoya et al. (1995) observed a small population of wild White-rumped Munias in Okinawa, Japan, and recorded two types of distance calls that may correspond to the sexually dimorphic calls of the Bengalese Finch. However, neither Restall (1996) nor Okanoya et al. (1995) described the details of sexual differences in distance calls; Restall (1996) did not show sonograms of the calls, and Okanoya et al. (1995) did not confirm the sex of the calling individuals.

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In the present study, we investigated the White-rumped Munia *L. s. phaethontoptila* in Taiwan, in order to establish a sexing method that can easily be applied in the field. We measured morphological characteristics and examined distance calls by ear in the field so as to sex individuals. The sexual difference in distance calls was confirmed by sonogram. Correct sex was determined in the laboratory (CHD gene analysis), and the accuracy of the two sexing methods (morphology and distance calls) was compared. Since monomorphic White-rumped Munias live in flocks throughout the year (Restall 1996), being able to sex individuals in the field will be indispensable for researchers investigating their ecology, social system, life-history, and breeding behavior.

METHODS

1) Field measurement of morphological characteristics

Fieldwork was conducted at a site near Antong hot spring (23°16'32.3"N, 121°20'40.0"E) in Hualien County, eastern Taiwan, from 16 to 18 February 2002. Antong hot spring is a hilly area, around 260 m above sea level. Mist nets were set in the morning (from 06:00 to 11:00), at a grassland area where a group of White-rumped Munias regularly foraged. The following characters of the birds captured were measured using digital calipers and a ruler: 1) flattened wing length (FWL), 2) longest tail length (LTL), 3) tarsus length (TSL), 4) entire culmen length (ECL), 5) bill width (BLW), and 6) bill height (BLH). BLW and BLH were measured at the anterior edge of the nostril. Each bird was also weighed (body weight BDW) using a digital balance.

The differences in morphological measurements between males and females were examined using the t-test. In order to establish the probability of successful sex determination using morphological measurements, both discriminant, and stepwise discriminant analyses were performed. SPSS statistical packages (SPSS 1993, 1994) were used for the statistical analyses.

2) Blood sampling and genomic sex determination

Small blood samples (20–60 µl) were obtained from each bird for subsequent laboratory analysis to determine sex using the CHD genes of DNA (Griffiths et al. 1996). In brief, PCR reaction volumes of 50 µl were made up of *taq* polymerase (Takara), 200 µm of each dNTP, P2, P3 primers, 100 mg of ge-

nomeric DNA and 0.15 units of *taq* polymerase. After PCR amplification, the restriction enzyme *HaeIII* was used to cut 8 µl of PCR product in Promega buffer 3 and 50 ng/µl bovine serum albumin in a total volume of 10 µl. Electrophoresis was then used to detect sexually dimorphic bands (see Fig. 2).

3) Sex determination by distance calls

Field determination

When the birds were released, they always gave distance calls. We recorded these calls using a directional gun microphone (AUDIO-TECHNICA AT815b) and a DAT recorder (TASCAM DA-P1). Distance calls were first examined in real-time (i.e., when the birds were released) by ear, by an experienced observer, Hiroko Yamada, who determined the sex of the caller in the field without consulting the DNA or morphological data.

Spectrographic determination

Sex determination, based on hearing calls, was further confirmed by spectrographic observation. Sonograms (sound spectrograms) of the calls were obtained using a digital signal processor (Avisoft version 3.93, SASLab Pro 2002) at a sampling rate of 48 kHz and a Fast Fourier Transform (FFT) size of 512 points (see Fig. 3). We counted the number of elements in each call and compared those of males and females determined by the DNA sexing data (see Fig. 2).

Individual variation

Individual variation in distance calls by each sex was also analyzed. We were able to record more than one call from several individuals. By taking a Pearson correlation coefficient between two matrices each derived from the sound spectrograph of a distance call, we were able to measure the similarity of the two calls (Avisoft version 3.93, SASLab Pro 2002). Eighteen calls recorded from six males and twelve calls recorded from four females were separately submitted to a furthest neighbor cluster analysis (StatPartner version 2.0, NEC software 1995) and a dendrogram reflecting the similarity among calls was calculated.

RESULTS

1) Morphological analyses

About 50 White-rumped Munias were found feeding on the ground at the study site, where they fed on

Table 1. Measurements of morphological characters (mm) and body weight (g) of male and female White-rumped Munias captured in eastern Taiwan in February 2002. Male: N=13, Female: N=12.

Measurements	Male		Female		t-value
	Mean±SD	Range	Mean±SD	Range	
Wing length	50.52±0.91	47.1–51.7	49.35±1.15	47.0–51.7	2.84*
Tail length	42.94±1.95	36.80–46.15	40.19±2.42	35.36–45.36	3.15**
Tarsus length	13.36±0.43	12.36–13.86	13.20±0.45	12.76–14.20	0.89
Bill length	10.53±0.37	9.94–11.12	10.55±0.31	9.86–11.19	0.13
Bill width	6.66±0.40	6.24–7.84	6.47±0.27	5.95–6.85	1.33
Bill height	7.17±0.30	6.66–7.73	7.05±0.18	6.68–7.54	1.31
Body weight	9.94±0.48	8.8–10.6	9.80±0.45	9.5–10.4	0.74

*P<0.01, **P<0.005

the seed of silver grass *Miscanthus* sp. In total, 26 birds were captured, measured, and blood samples taken, during three days in February 2002. From the DNA analysis, 13 birds were identified as males, and 13 as females. As one female was molting her tail feathers, measurements of 13 males and 12 females were used for the following morphological analyses. Males had significantly longer tails and wings than females, although considerable overlaps were observed between the sexes Fig. 1.

The probability of correct discrimination of the preliminary discriminant analysis was 76.0% (19/25). To simplify the function and to distinguish between the sexes more precisely, the increasing stepwise discriminant analysis was performed. Two variables, tail length (LTL) and wing length (FWL), were included in the analysis. The resulting discriminant function is as follows:

$$D = 0.32 \text{ LTL} + 0.60 \text{ FWL} - 43.41$$

(Wilks' $\lambda = 0.59$, $\chi^2_{1,25} = 11.55$, $P < 0.005$; Fig. 1).

The two variables contributed to the function significantly (LTL: Wilks' $\lambda = 0.70$, $F_{1,23} = 9.92$, $P < 0.005$, FWL: Wilks' $\lambda = 0.59$, $F_{2,22} = 7.60$, $P < 0.005$). $D > 0$ indicates that the individual is male and $D < 0$ indicates that it is female. The probability of correct discrimination among males was 92.3% (12/13), and 75.0% (9/12) among females. For both sexes, the probability was 84.0% (21/25).

2) Genomic sex determination

Genomic DNA from individual White-rumped Munias was cut using the restriction enzyme *HaeIII* and the resulting electrophoretic bands were used to determine the sex (Fig. 2). For example, in sample

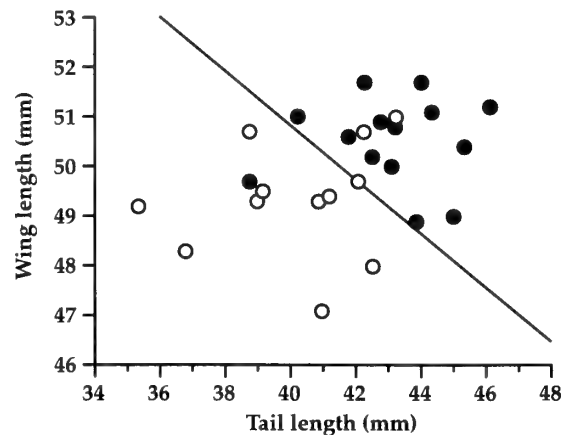


Fig. 1. Relationship between the tail length and wing length of White-rumped Munias. Open circles indicate females, closed circles indicate males. The line indicates the boundary between males and females ($D=0$, $D=0.32 \text{ LTL} + 0.60 \text{ FWL} - 43.41$; LTL: tail length, FWL: wing length).



Fig. 2. Comparison of sex determination by ear in the field, and by CHD genes in the laboratory. Data from 24 individuals are shown.

No. 1, the 110bp band was absent so this was determined as a male. In sample No. 3 the CHD gene product remained and this was identified as a female.

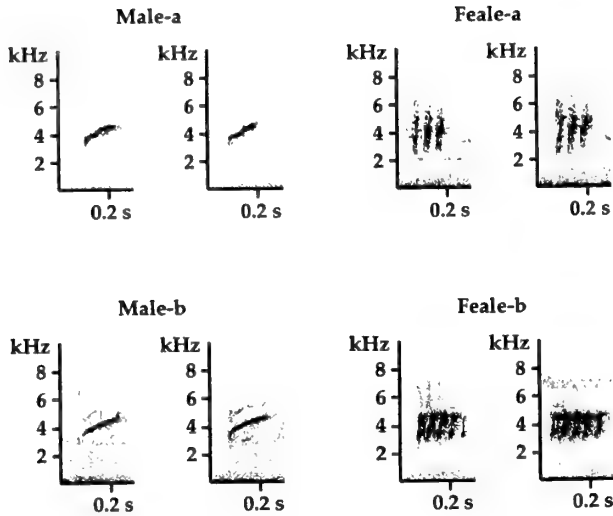


Fig. 3. Sample sonograms of calls recorded at Antong hot spring. Two calls are shown for each individual and data from two birds of each sex are shown to illustrate sex differences and individual distinctiveness of the call.

3) Distance calls

Field determination

Distance calls were classified in the field by Hiroko Yamada, based on previous studies of the distance calls of Bengalese Finches (Okanoya & Kimura 1993) and of White-rumped Munias (Okanoya et al. 1995). She classified a high-pitched, continuous, clear call, as that of the male, and a low-pitched, pulsed, noisy call as that of the female. Based on these calls, we temporarily identified the sex of the 26 individuals captured to be 13 males and 13 females. This classification perfectly matched the DNA sexing data (Fig. 2).

Spectrographic comparisons and individual variation

Spectrographic analyses and DNA sexing confirmed the subjective classification of male and female calls (Fig. 3). The average number of elements in the call was one in males and 3.67 in females (Fig. 4).

Results of the cluster analysis revealed that calls of each individual are quite distinctive, roughly forming one cluster each (Fig. 5) both in males and in females. Thus, the distance calls of the White-rumped Munia are not only sexually, but also individually distinctive.

DISCUSSION

To establish an efficient way of sexing wild White-

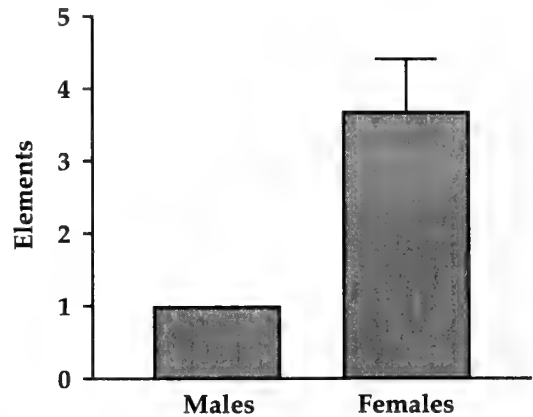


Fig. 4. The average number of elements in the calls of males ($N=13$) and females ($N=13$). The vertical bar indicates standard deviation.

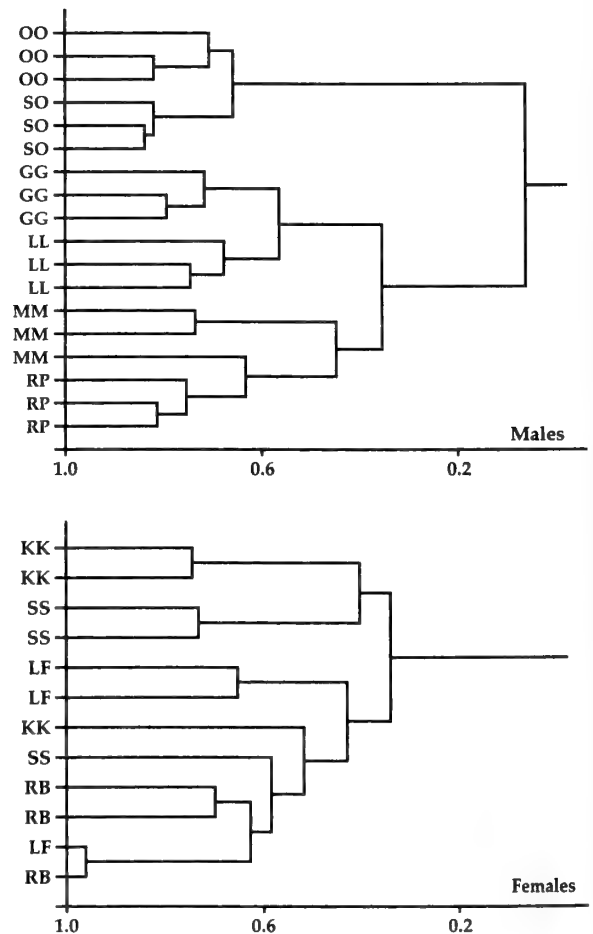


Fig. 5. For each sex, spectrographic correlations were calculated among multiple calls of several individual birds. The resulting correlation matrix was analyzed using a furthest neighbor cluster analysis and expressed using a dendrogram. The letters indicate individuals identified by a unique combination of color rings.

rumped Munias, several physical measurements were made in the hand. Sex was also determined based on the acoustic characteristics of an individual's calls. These measures were compared with the results of sexing based on the CHD gene.

DNA analysis confirmed that the White-rumped Munia gives sexually dimorphic distance calls, as has previously been shown for the domestic Bengalese Finch (Yoneda & Okanoya 1991; Okanoya & Kimura 1993) and as has been suspected of wild White-rumped Munias (Restall 1996).

Two morphological characters, wing length and tail length, also differed significantly between males and females, however, there was also considerable overlap in the range of these measurements between the sexes. The increasing stepwise discriminant analysis, using wing and tail measurements, correctly sexed only 84.0% of individuals. The probability of sex discrimination would be even lower during the molting season when tail and wing measurements become less reliable. Therefore, it is concluded that the difference in distance calls is the most useful trait for easily distinguishing sex in the field.

Sexual differences in distance calls have been well studied in one particular estrildid species, the Zebra Finch *Taeniopygia guttata*. Zann (1984) suggested that the main function of distance calls is to maintain the pair bond throughout the year. The sexual difference in such calls, when compared with monomorphic calls, is thought to double the probability of finding the partner when the pair is separated in vegetation or in a large conspecific flock (Zann 1984). Blaich et al. (1996) proved Zann's hypothesis by laboratory experiment, by showing that both male and female pair-bonded Zebra Finches used distance calls to initiate and maintain contact with their mates when they were physically separated. Blaich et al. (1996) also observed that unpaired Zebra Finches did not use distance calls to interact with other conspecifics.

The function of distance calls has not yet been described in the White-rumped Munia, however, in the Bengalese Finch, Okanoya and Kimura (1993) showed that the sexual difference in distance calls is readily perceived by conspecifics. In all probability, wild White-rumped Munias are also able to perceive the sexual difference in distance calls. They live in densely vegetated areas and form flocks as Zebra Finches do. It is possible that the distance call of the White-rumped Munia also serve to enable individuals to maintain contact with other flock members that are not in sight.

Given that there is a distinct difference in distance calls between the sexes, and given that the domesticated Bengalese Finch can perceive sexual differences between calls, it is suggested that distance calls in the wild White-rumped Munia allow members of pairs to remain in contact.

We have established that the two different distance calls of males and female White-rumped Munias can be easily perceived by a trained observer in the field. We have also shown, by acoustical analysis, that distance calls are not only sexually dimorphic, but also individually distinctive. It should be possible for a trained observer to identify individuals by call in the field. Thus, the distance call of the White-rumped Munia is a powerful tool during field investigation of this species.

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ORIGINAL ARTICLE

Comparative study of territoriality and habitat use in syntopic Jungle Crow (*Corvus macrorhynchos*) and Carrion Crow (*C. corone*)

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Abstract Jungle Crows (*Corvus macrorhynchos*) and Carrion Crows (*C. corone*) are common species in Japan. They are closely related and considered ecological “generalists”. I carried out a comparative study on territory and habitat use of these crows in an area where they occur syntopically. The two species defended their territories both intra- and interspecifically. The feeding behavior on the ground and the microhabitats in the territories differed between the species. Jungle Crow territories contained more urban areas, and they foraged mainly at garbage stations. In contrast, Carrion Crows mainly foraged in natural or at least un-paved microhabitats and stayed longer on the ground. Differences in microhabitat use and feeding behavior seemed to contribute to ecological separation between the two species of crows.

Key words Carrion Crow, Feeding behavior, Habitat segregation, Interspecific territory, Jungle Crow

Ecological segregation in sympatric or syntopic birds has often been studied. For example, several syntopic tit species have been shown to be ecologically separated by differences in their vertical utilization of trees and by different feeding methods (Nakamura 1978). However, in generalist species that use a wide variety of foods without clear specialization in feeding behavior, separation mechanisms have been poorly studied (Loyn 2002).

Corvids are typical generalists (Goodwin 1982). Jungle Crows (*Corvus macrorhynchos*) and Carrion Crows (*C. corone*) are the most common corvid species in Japan. They occur in all parts of Japan, except for Okinawa where Carrion Crows are absent.

Jungle Crows and Carrion Crows occur sympatrically, although habitat segregation has been reported. Jungle Crows primarily inhabit forests, but also cities and coastal areas. Carrion Crows inhabit cultivated fields, river floodplains, and coastal areas. Higuchi (1979) suggested that Jungle Crows prefer environments with an abundant supply of garbage or carcasses, and thus they occur preferentially in cities and coastal areas. Nakamura (2000) suggested that the

home ranges of Carrion Crows include more cultivated fields than those of Jungle Crows in the same area. Heinz (1989) reported that the growth rate of chicks of Carrion Crows is higher in agricultural habitats than in urban habitats, and he suggested that agricultural habitats provide better food conditions. However, in small towns where the two species occur syntopically in the same habitat (Tamada & Fujimaki 1993; Takahata et al. 1996; Nakamura 2000), differences in microhabitat use, such as feeding sites, have not been studied sufficiently.

Differences in feeding habits and interspecific territoriality have both been suggested as separation mechanisms between syntopic species (Loyn 2002). In a study of food preferences of Jungle Crow and Carrion Crow, Ikeda (1957) analysed stomach contents of the two species and suggested that Jungle Crows prefer meat and tree fruits, whereas Carrion Crows prefer crops. However, the differences in feeding habits were insufficient to clarify the separation mechanism because 1) the food habits largely overlapped and 2) all birds were shot in cultivated fields, thus the food habits of the two species may be different in different habitats; information on actual feeding habitats and behaviour were lacking.

If food or microhabitat preferences of the two

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species were separated, their feeding behavior and feeding sites should differ. If the feeding habits overlapped to a certain extent, resource competition would occur and they should defend resources interspecifically. Previous studies on territoriality have dealt mainly with only one species (Haneda & Iida 1966; Kuroda 1974, 1981; Nakamura 1998). Interspecific territoriality has been poorly studied.

I carried out a comparative study on the habitat use of Jungle and Carrion Crows where they occur in the same habitat. I describe the intra- and interspecific territoriality and the behavioral differences between the species with respect to feeding behavior.

MATERIALS AND METHODS

I conducted the study in the eastern part of Kyoto City, Kyoto Prefecture, Japan (35°01'N, 135°46'E). The study site covered an area of 1.5×1.0 km and was located in an urban environment. It included residential areas, a small forest in the grounds of a Shinto-shrine, rivers, and a university campus. The rivers ran through narrow floodplains consisting of cobbles, which in many areas were covered with grasses. I focused on two study sites: one was around Shimogamo-shrine and the other around Kyoto University. I combined the data from these two sites in the following analysis. The study was conducted during the breeding season (from the incubation period in March until the young fledged in July) in 1998.

Eleven pairs of Jungle Crows and 17 pairs of Carrion Crows were found in the study area. I used seven pairs of Jungle Crows (J1~J7) and 12 pairs of Carrion Crows (C1~C12) in the following analysis and excluded four (J8~J11) and five (C13~C17) pairs of the Jungle and Carrion Crows, respectively, from the quantitative analysis because there were fewer observations for these. The territories of the excluded pairs are also shown in figures 1 and 2 because they seemed to inhabit the same place throughout the study period, although these territories were not completely determined.

Individual crows were not ringed because no efficient method of capturing breeding adults has been developed.

I tracked individuals leaving the nests until they were lost, or tracked individuals found in other places until they visited their nests. The home range was estimated by connecting the outermost points of sightings belonging to one particular pair (convex polygon method). While tracking individual birds in their

home ranges, I recorded locations of antagonistic behavior against intruders. The types of antagonistic behavior distinguished included loud calls (Kuroda 1974, 1990), parallel flight with intruders and chasing, threatening or attacking intruders. A territory was defined as the area defended by a particular pair. A territorial boundary was determined by connecting the outermost points at which antagonistic behavior by the territory owners was observed. I also recorded the horizontal and vertical locations of other types of behavior (perching, resting, feeding). If crows threatened and chased the observer for longer than five minutes, tracking was stopped and the territory was left to avoid disturbance.

Observations were made from morning (c. 30 min. before dawn at the earliest) to sunset, on 2–4 days per week. All tracking data included tracking during early morning, when human food scraps were most readily available for the crows. Individual crows occasionally disappeared from sight and had to be searched for, so that the tracking record was not continuous. The area of home ranges and territories did not change after six hours of successful tracking data in total. Therefore, they were defined after this observation period. Two or three days were needed to detect each nest and accumulate sufficient tracking data to determine one territory. Therefore the reproductive stages of pairs during observations were not synchronized. The size of three Carrion Crow territories that was determined early in the season did not change throughout the observation period. During the following analysis it was assumed that seasonal changes in territory size were negligible.

For the quantitative analysis of habitat use, a habitat map based on a mesh with 20×20 m quadrats was produced. The number of quadrats in which crows foraged was compared among pairs, focusing on feeding sites and their dispersal.

All feeding quadrats that a pair foraged was recorded and pooled. The distance between two nearest quadrats in which foraging behaviour was observed was calculated by the following equation: $D = \sqrt{(X+1)^2 + (Y+1)^2}$ with X representing the number of quadrats between the observation points in horizontal direction and Y representing the number of quadrats in vertical direction. Therefore, if two quadrats were located next to each other ($X=0$ and $Y=0$), the distance was 1. If the quadrats forming several separated clusters, the smallest distances between clusters are also measured. The distance between two clusters was analyzed as the same as the

distances within the clusters. When the quadrates that crow used forming several clusters, the distances between the clusters indicate the minimum distances that the individual must travel to the feeding site located in other cluster. Thus, the distance between nearest feeding quadrats within the same cluster and the smallest distance between the clusters were measured. In this analysis, if the distance between two quadrats is 1, that indicates these quadrats form a cluster in which a crow can feed.

The distances measured in one territory were pooled and the mean distance was calculated.

The area of certain types of environment in each territory was estimated based on the number of quadrats belonging to each type. The following categories were distinguished: forests, river floodplains, grasslands outside river floodplains, open gravel areas, and urban areas. "River floodplain" included open water, riverbeds covered with cobbles and grassland. Forests, grasslands, rivers, and open lands together were considered as environments rich in natural food sources such as insects or acorns. On the other hand, urban areas were considered as a type of environment poor in natural but rich in man-made food sources, i.e. garbage. During the data analysis only two types of contrasting environments were considered: Natural environment (forest, river floodplain, grassland outside river floodplains, open area) and urban environment.

RESULTS

1) Intra- and interspecific territoriality

Both intra- and interspecific intrusions caused the territory owners to display antagonistic behavior (Table 1). In Jungle Crows, antagonistic behavior was most frequently observed towards Carrion Crows and next frequently, against Jungle Crows. In Carrion Crows, the most frequently observed opponents were Jungle Crows, with the Black Kites (*Milvus migrans*) and Carrion Crows following in this order. However, it was impossible to record all intrusions while ob-

serving one individual because this study focused on a behavioral comparison between the two crow species. Therefore, the total frequency of intrusions by all species against which antagonistic behavior was shown is unknown. Thus, the observed ratio of antagonistic behavior by each crow species against all other species does not reflect simply the extent of the crows' aggressiveness against each intruder species. Other intruder species occurred, such as humans, domestic cats (*Felis catus*), Black-headed Gulls (*Larus ridibundus*), Northern Goshawks (*Accipiter gentilis*) and Eurasian Wigeon (*Anas penelope*). Northern Goshawk was observed only once during the study period. Cats were not frequently encountered, but they were almost invariably attacked when they entered a crow's territory. Other species were frequently present but generally did not trigger antagonistic behaviour, however, a wigeon swimming in the river was attacked by a Carrion Crow for no apparent reason.

No intraspecific overlapping of territories was recorded (Figs. 1 and 2). Interspecific overlapping was observed between the territory of C3 (Carrion Crow) and those of J1 and J2 (Jungle Crow). However, the owner pairs of J1 and J2 never foraged or perched in C3's territory although they were observed flying over it. J1 and J2 did not behave antagonistically within the C3 territory; therefore the territories of J1 and J2 were drawn as concave polygons (see Fig. 1). The area that crows used but did not defend was defined as their home range.

Notable cases involving overlapping of home ranges between the two species were observed. The home ranges of J2 and J4 largely overlapped the home ranges of Carrion Crows above the Takano River. The nest of J4 was located on the western side of the Takano River, but the J4 pair foraged mainly on the eastern side. The J2 and J4 pairs did not perch or forage in the river area. Flying over the Takano River resulted in intrusions by the J4 pair into the territory of the C7 pair. In 53 cases, the C7 pair showed no reaction to the Jungle Crows' passing, but in 10

Table 1. Frequency of antagonistic behaviors (rate per hour) in Jungle and Carrion Crow.

Resident	Intruder species						
	Jungle Crow	Carrion Crow	Crow spp.	Black Kite	Egret spp.	Cat	Unknown
Jungle Crow	0.44	0.64	0.16	0.27	0.04	0.03	0.56
Carrion Crow	0.83	0.27	0.08	0.66	0.07	0.03	0.21

cases they chased or attacked the intruders. The Jungle Crows never attacked the C7 pair above the river. When being chased or attacked by the territory owners, the Jungle Crows never engaged in fighting but just flew away. Immediately after passing the territory boundary to one side of the river, the Jungle Crows turned and started threatening or attacked the Carrion Crows that were chasing them. A similar case, in which a Jungle Crow pair did not defend part of their home range, and that undefended area was occupied by a territorial Carrion Crow pair, was also observed

between the J2 and C5 pairs (Table 2) whose home ranges also overlapped. As in the case of J4 and C7, J2 foraged on the opposite side of the river. The frequency of Carrion Crow attacks on Jungle Crows crossing the river, where the Carrion Crows held territories, did not differ significantly between pairs J2 and J4 (Table 2, Fisher's exact test, two-tailed, $N=24$ (J2), 66 (J4), $P=0.40$, NS), although the sample size is small. Four garbage collection points ("garbage stations") were located in the foraging area of J4 on the eastern side of the river (Figs. 1 and 3). The garbage stations were uncovered, thus the garbage in plastic bags was easily accessible for the crows. J2 also visited three to four garbage stations. Compared with the western side, there were more apartment houses on the eastern side of the Takano River where garbage was placed in the garbage stations everyday. Although J3 did not fly across the river, the pair flew

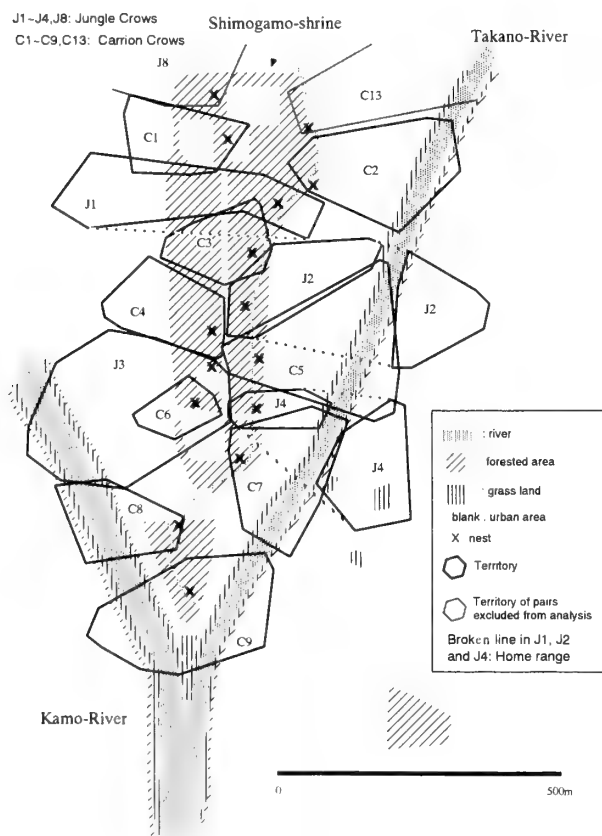


Fig. 1. Territories of Jungle Crows and Carrion Crows at the Shimogamo-shrine study site in the western part of the study area. Broken lines connecting the split territories of J2 and J4 show the home ranges of the pairs. J8 and C13 were not included in further analysis.

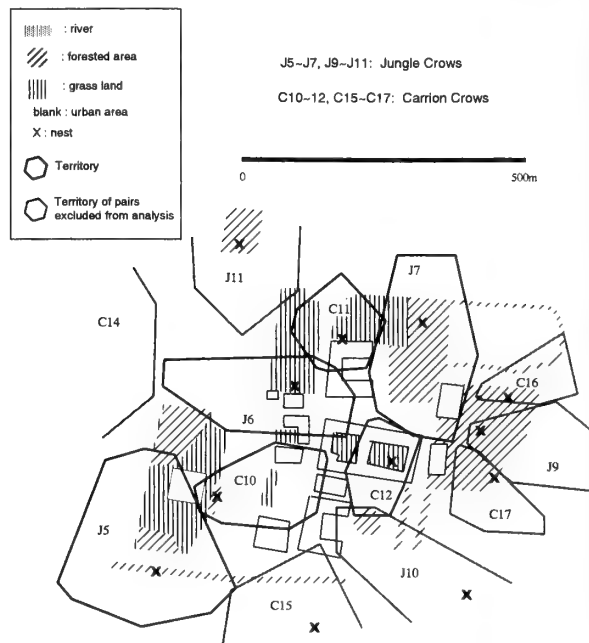


Fig. 2. Territories of Jungle Crows and Carrion Crows in the Kyoto University study site in the eastern part of the study area. J9~J11, and C14~C17 were not included in further analysis.

Table 2. Observed interactions when Jungle Crows passed across a Carrion Crow's territory. Figures in table show the occurrence frequencies. Note that attacks to the owner is 0.

Intruder	No interaction	Attack to owner	Attack to Black Kite	Attacked by owner	Total
J2	22	0	0	2	24
J4	53	0	3	10	66

Table 3. Time spent on the ground (min). Number of touchdowns indicates the frequency that crows flew down to the ground.

Species	Observation duration	Number touchdowns*	Duration on the ground					
			Total duration*	% per observation	Mean duration*	Min. duration	Max. duration	SD
Jungle Crow	1800	96	120	6.6	1.3	0.5	5	0.88
Carrion Crow	1908	181	693	36.3	3.8	0.5	23	3.52

* Indicates a significant difference between the species (Mann & Whitney's U test, $P < 0.05$).

over C6's territory to visit garbage stations on the southwestern side of the J3 territory. The C6 pair attacked the J3 pair when they flew over C6's territory. The J3 pair seemed to mostly attack the C6 pair at the territory border as did the J2 and J4 pairs. However, the J3 and C6 pairs were sensitive to the observer and nested in dense woods where observation from a distance was impossible, thus further interactions between the pairs could not be investigated.

This type of split territory was not observed in Carrion Crows. All Carrion Crow territories were continuous, and they stayed inside the areas they defended. Carrion Crows' home ranges coincided with their territories (Figs. 1 to 2).

2) Time spent on the ground

A prominent behavioral difference between the two species was the use of different vertical positions within the habitat. Jungle Crows mainly stayed on trees, buildings, utility poles, or power lines, that is, places higher than the ground level. I classified the perching positions into two levels, ground level, and higher level. Jungle Crows used the ground level in only 6.6% of the observation time, whereas Carrion Crows were on the ground during 36.3% of the observation time (Table 3). Jungle Crows stayed on the ground for 5 min at the longest, whereas Carrion Crows stayed for up to 23 min. The mean duration was 1.3 and 3.8 min for Jungle and Carrion Crows, respectively, which is a significant difference (Table 3, Mann-Whitney U-test, $N=96$ (Jungle Crow) and 181 (Carrion Crow), $U=3253$, $P < 0.001$). The frequency of flying down to the ground was also significantly lower in Jungle Crows (Table 3, Mann-Whitney U-test, $N=96$ (Jungle Crow) and 181 (Carrion Crow), $U=10$, $P < 0.001$).

3) Comparison of feeding sites

Mean distances between feeding quadrates were significantly larger in Jungle Crows than in Carrion

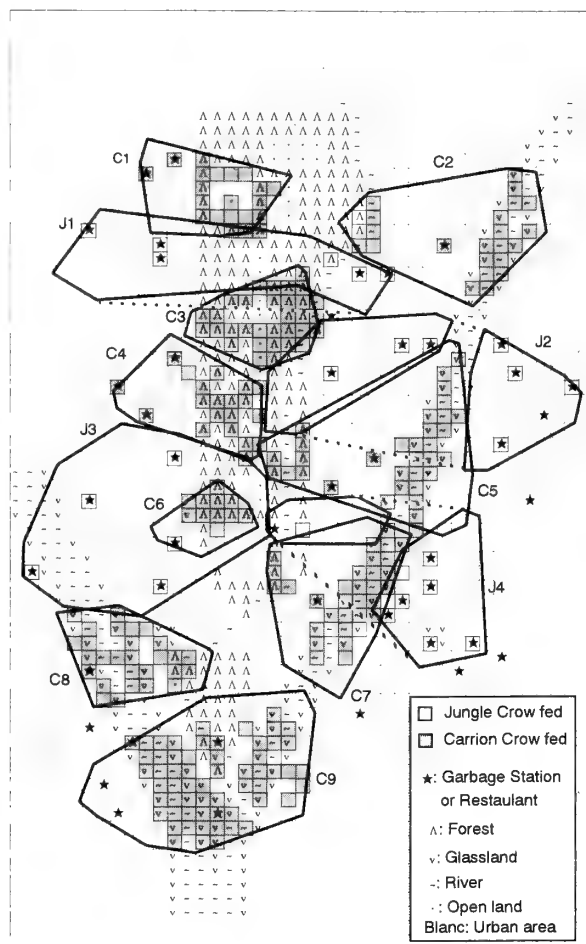


Fig. 3. 20×20 m mesh quadrats were laid over Fig. 1 for quantitative estimation of areas of feeding sites and dispersal. Solid quadrats show the feeding sites used by the crows. Polygons show the territories.

Crows (Figs. 3 and 4, Tables 4 and 5, Mann-Whitney U-test, $N=45$ (Jungle Crow) and 317 (Carrion Crow), $U=0$, $P < 0.001$). In Carrion Crows, the mean distance was nearly 1, indicating that Carrion Crow feeding sites are continuous and form a small number of large clusters. On the other hand, in Jungle Crows

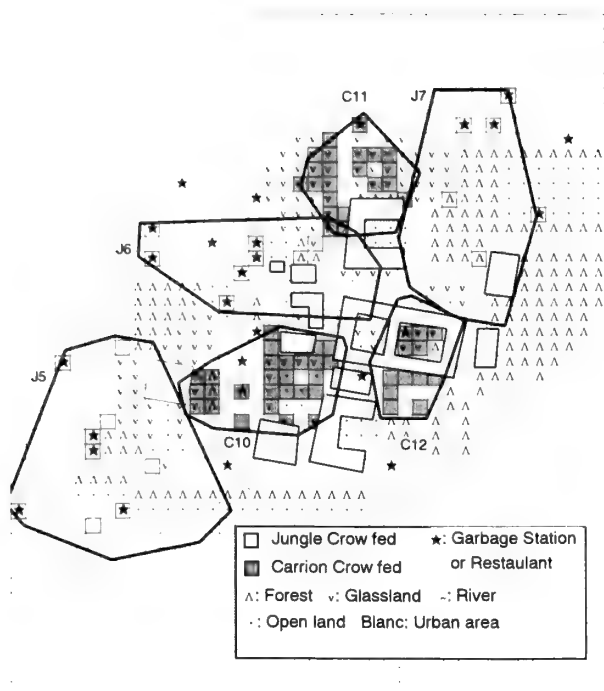


Fig. 4. 20×20m mesh quadrats were laid over Fig. 2 for quantitative estimation of areas of feeding sites and dispersal. Solid quadrats show the feeding sites used by the crows. Polygons show the territories.

the distances ranged from 1 to 15, indicating that Jungle Crow feeding sites are dispersed, and form isolated, small clusters (or consist of isolated single quadrats).

Jungle Crows used a small number of feeding quadrats. The number of feeding quadrats in Carrion Crows was significantly larger than in Jungle Crows (Tables 4 and 5, Mann-Whitney U-test, $N=7$ (Jungle Crow) and 12 (Carrion Crow), $U=0$, $P<0.001$). Jungle Crows had larger territories than Carrion Crows (Tables 4 and 5, Mann-Whitney U-test, $N=7$ (Jungle Crow) and 12 (Carrion Crow), $U=10.5$, $P<0.01$), and accordingly the feeding site density was significantly lower in the former than in the latter (Table 4, Table 5, Mann-Whitney U-test, $N=7$ (Jungle Crow) and 12 (Carrion Crow), $U=0$, $P<0.001$). These results indicate that Jungle Crows use a smaller number of more dispersed feeding sites in larger territories than Carrion Crows.

In Jungle Crow territories, the frequency of quadrats occupied by urban area was higher than in those of Carrion Crows (Fig. 5, Mann-Whitney U-test, $N=7$ (Jungle Crow) and 12 (Carrion Crow), $U=12$, $P<0.05$). The location of large garbage stations (more than 2×2 m in size) and restaurants

Table 4. Characteristics of feeding site distributions in Jungle Crows. See also Figs. 3 and 4

Pair	No. feeding quadrats	Mean distance (No. quadrats)	Territory size (ha)	Quadrat density (quadrat/ha)
J1	5	5.20	2.07	2.42
J2	7	4.29	6.32	1.11
J3	6	4.67	6.18	0.97
J4	10	4.50	5.64	1.77
J5	9	3.80	6.12	1.47
J6	8	4.00	6.38	1.25
J7	6	2.63	3.57	1.68
Mean	7.29	4.16	5.18	1.52
Min	5	2.63	2.07	0.97
Max	10	5.20	6.38	2.42
SD	1.80	0.82	1.69	0.49

Table 5. Characteristics of feeding site distributions in Carrion Crows. See also Figs. 3 and 4

Pair	No. feeding quadrats	Mean distance (No. quadrats)	Territory size (ha)	Quadrat density (quadrat/ha)
C1	19	1.37	2.07	9.18
C2	24	1.38	3.43	7.00
C3	31	1.03	1.59	19.50
C4	27	1.30	2.38	11.30
C5	37	1.11	4.05	9.14
C6	13	1.15	1.13	11.50
C7	23	1.41	3.51	6.55
C8	29	1.14	1.96	14.80
C9	43	1.13	4.11	10.50
C10	29	1.11	3.17	9.15
C11	21	1.10	3.37	6.23
C12	13	1.15	2.10	6.19
Mean	25.75	1.20	2.74	10.09
Min	13	1.03	1.13	6.19
Max	43	1.41	4.11	19.50
SD	8.94	0.13	0.99	3.92

(garbage was available everyday) where the crows can feed on garbage are shown in Figs. 3 and 4. The frequency of feeding at garbage stations among all feeding quadrats was significantly higher in Jungle Crows than in Carrion Crows (Fig. 6, Mann-Whitney U-test, $N=7$ (Jungle Crow) and 12 (Carrion Crow), $U=0$, $P<0.001$). In the former case it accounted for 81.2%, but in the latter only for 6.4%. However, the extent to which the species depended on garbage

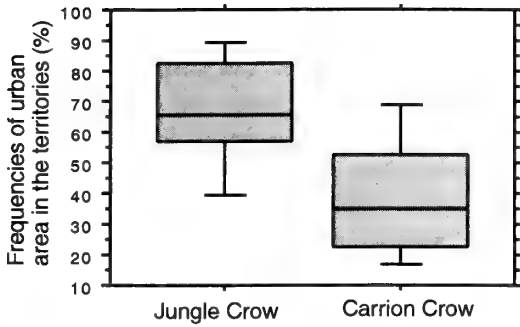


Fig. 5. The proportion of urban areas in the territories of Jungle Crows and Carrion Crows calculated from the number of quadrats. The proportion is larger in Jungle Crows than in Carrion Crows (Mann-Whitney U-test, $P < 0.05$). The boxes, the lines inside the boxes and the bars indicate 50% of samples, median and standard error, respectively.

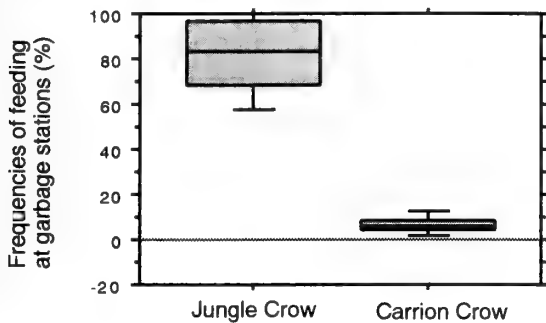


Fig. 6. The frequencies of feeding in quadrats containing garbage stations among all feeding quadrats. The frequency is higher in Jungle Crows than in Carrion Crows (Mann-Whitney U-test, $U = 0$, $P < 0.001$). Boxes, lines inside boxes and bars indicate 50% of samples, medians and standard errors, respectively.

could not be estimated because the type and amount of food items taken up by the crows were unknown in many cases.

DISCUSSION

Jungle and Carrion Crows defended their territories both intra- and interspecifically. This territoriality indicates that intrusions both of members of the same species and of different species have negative consequences for the territory owners. Crows attacked many species, but the extent of aggressiveness against each attacked species is uncertain. Because the territories of the two species of crows tended to be distributed alternately, the frequency of antagonistic behavior between them could be expected to be high. Each territory of each species was adjacent to

territories of the other species, which meant that conflicts could more easily occur between the species than among members of the same species. Carrion Crows attacked Black Kites more frequently than Jungle Crows did, possibly because Black Kites were usually observed flying over the Kamo River and the Takano River, where Carrion Crow territories were situated. In the cases when Black Kites intruded into Jungle Crow territories, the Jungle Crows also attacked the kites aggressively.

The mean duration of terrestrial feeding is significantly smaller in the Jungle Crows. The frequency of flying down to the ground is also significantly smaller, and therefore the total duration of terrestrial feeding is significantly smaller in the Jungle Crows. This difference in feeding behavior between the two species has not been quantitatively estimated in previous studies. The difference in feeding behavior coincides with their microhabitat preferences; i.e. the longer time spent on the ground by Carrion Crows coincides with their utilization of natural ground surfaces as feeding sites.

The microhabitat composition of the territories differs between the species. The proportion of urban areas is significantly higher in the territories of Jungle Crows than in those of Carrion Crows. The same tendency was also found in previous studies (Higuchi 1979; Nakamura 1998).

The use of feeding habitats differs between the species. Jungle Crows use isolated, small sites within larger feeding areas. Carrion Crows, in contrast, use large, continuous areas within feeding areas. This difference relates to the differing amounts of time spent foraging on the ground between the two species, and their foraging habits (Jungle Crows commonly drop to take food spotted from a vantage point, while Carrion Crows commonly forage on foot). The feeding sites of Jungle Crows are mainly garbage stations, but those of Carrion Crows are located in various environments, such as forest floors, grasslands, and river floodplains in addition to a small number of garbage stations. It is suggested that the difference in feeding microhabitats results from an inverse relationship between territory size and the number of feeding quadrats. Jungle Crows feed mainly on human food scrap at a small number of good feeding sites where they can easily access food and feed, such as at large garbage stations. In contrast, Carrion Crows used various microhabitats and spend longer on the ground in each, therefore Carrion Crow territories are smaller but the number of feeding quadrats is larger than in

Jungle Crows; Carrion Crows, it seems, are able to find food resources in any microhabitat.

Jungle Crows in urban areas have been suggested to depend on organic waste (e.g. Higuchi 1979). Carrion Crows also forage at garbage stations, although this behaviour is less frequent. It appears that waste is not the main food resource for Carrion Crows in the study area. Small garbage stations, which are not shown in Figs. 3 and 4, are situated in urban areas. However, the territories of Carrion Crows contain less urban area than those of Jungle Crows, therefore the number of such small garbage stations is probably lower in Carrion Crow territories. The different proportions of urban areas in the territories of the two species are most likely related to differences in microhabitat preferences and feeding behavior. Another possibility is that Jungle Crows include sufficient garbage stations within their territories to provide all their food resources, thus they do not need to forage in other microhabitats as Carrion Crow do.

The split territories observed in two pairs of Jungle Crows in this study, were probably caused by the particular pattern of resource distribution and the defence cost. Territoriality is adaptive when the benefit by exclusive use of the area is larger than the defence cost (Maynard Smith 1982); the Takano River is a resource-poor microhabitat for Jungle Crows, and it would be too costly to exclude territorial Carrion Crows. On the other hand, riverbeds are valuable habitats for Carrion Crows, which implies that the same type of environment can have asymmetrical value for the two species. If food resources that Jungle Crows prefer, such as food scraps or carcasses, are found inside a Carrion Crow territory where it overlaps with a Jungle Crows' home range, resource competition between the species may occur. I observed that both Jungle Crows and Carrion Crows fed on food scraps at several garbage stations in a commercial area in Kyoto City, and the Jungle Crows dominated the food in several cases (Matsubara, unpublished data). This suggests that the two species compete for this food resource to a certain extent.

As demonstrated above, feeding habitats and feeding behavior differ between the two species, but as indicated in a previous study (Ikeda 1957), their food preferences largely overlap. Jungle Crows are likely to be dominant over Carrion Crows because they are larger: the body weight range of the former is 570–860 g, and that of the latter is 370–730 g (Tamada & Fujimaki 1993). Another potentially important issue is nest defence, because corvids are known to prey on

other bird's nests. Nest predation by conspecific young individuals has been suggested to be the main reason for reproductive failure in Carrion Crows (Yom-Tov 1974). I observed one case of a Jungle Crow attempting to predate a Carrion Crow's nest (Matsubara, unpublished data). In Tokyo, successful nest predation by Jungle Crows upon Carrion Crows' nests has been reported (Hitoshi Fujimura, personal communication). Thus, interspecific territoriality between Jungle Crows and Carrion Crows may partly be due to food resource defence and partly to nest defence. The differences in feeding behavior and habitat preference probably reduce resource competition, but apparently they are insufficient to avoid competition for food entirely. It is suggested that Carrion Crows in the study area are excluded from zones with abundant supply of organic waste because these are occupied by the dominant Jungle Crows; Carrion Crow territories probably do not offer enough garbage as a food resource for Jungle Crows to exclude Carrion Crows. However, Jungle Crows can be strong competitors for Carrion Crows if food that is attractive for Jungle Crows is found inside Carrion Crow territories. Interspecific territoriality and overlapping home ranges are likely to be maintained by the differences of feeding behavior, food habits and the distribution of food resources between microhabitats.

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ORIGINAL ARTICLE

Reduction of cost of polygyny by nest predation in the Black-browed Reed Warbler

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Abstract When female birds choose already-mated males as their mates, they suffer some costs. One major cost is a reduction in male parental care. However, since nest predation disturbs the nesting cycles of polygynously mated females, it might change the allocation of male parental care between the females. I investigated the effect of nest predation on the relationship between female mating order and their brood status during the nestling-rearing period in the Black-browed Reed Warbler *Acrocephalus bistrigiceps*. Polygynous males did not feed later-hatched broods. The nest predation rate was high (56% of nests), which gives subsequently mated females a chance to receive male assistance. Four subsequently mated females acquired monogamous status by the time their eggs hatched, because the previously mated females had failed in their breeding attempts and disappeared from the territories. In addition, a subsequently mated female's nest was preyed upon and her re-nesting delayed her own nesting cycle, which resulted in the disappearance of the previously mated female with her fledglings and gave monogamous status at egg-hatching to the subsequently mated female. Furthermore, a case of inversion in the hatching order in polygynously mated females occurred by the prolonged pre-laying period of the previously mated female, which resulted in the subsequently mated female obtaining primary status at egg-hatching. As a result, 43% of the females that paired with already-mated males acquired monogamous or primary status at egg-hatching, whereas 69% of the females that paired with unpaired males did so. This suggests that nest predation reduces the cost of polygynous mating in this reed warbler population.

Key words *Acrocephalus bistrigiceps*, Cost of polygyny, Male parental care, Mate choice, Nest predation

When female birds choose already-mated males as their mates, they suffer some costs (Verner & Willson 1966; Orians 1969). One of the major potential costs is a reduction in male parental care (Verner 1964; Orians 1969). Feeding by polygynous males decreases in later-hatched broods, or in broods of subsequently mated females (Martin 1974; Patterson et al. 1980; Alatalo et al. 1982; Dyrce 1986; Muldal et al. 1986; Bruun et al. 1997). When nesting cycles of polygynously mated females proceed smoothly, a female that chooses an already-mated male as her mate will be a parent of the later-hatched brood, and will incur the cost of reduced male assistance.

Nest predation is one of the major interruptions of the normal nesting cycle (Ricklefs 1969; Martin

1993) and changes the allocation of male parental care between previously and subsequently mated females (Temrin & Jakobsson 1988; Urano 1990). If a previously mated female fails in her breeding attempt and does not re-nest within the male's territory, the subsequently mated female will receive male parental assistance exclusively. Therefore, the frequency of nest predation influences the probability that subsequently mated females receive male assistance. To evaluate the cost of polygyny in a population, it is important to know both the nest predation rate and the relationship between female mate choice (whether an unpaired male or an already-mated male) and their brood status during the nestling-rearing period.

I studied the effect of nest predation on the allocation of male parental care in the Black-browed Reed Warbler *Acrocephalus bistrigiceps*. This paper pres-

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ents data showing how polygynous males assist in caring offspring. I also report the percentage of females that become mothers of assisted broods when they pair with unpaired or already-mated males. Finally, I discuss the extent of effect of nest predation on the cost of polygyny in this species.

METHODS

1) Study area and species

This study was conducted during the 1993–1997 breeding seasons in a 42.4-ha area of rice fields along the Arakawa River (36°52'N, 139°35'E; 8 m asl) in central Honshu, Japan. The study area included patches of scattered grassland, which consisted mainly of the common reed *Phragmites communis* and goldenrod *Solidago altissima*. The grassland is the breeding habitat of Black-browed Reed Warblers. The environment of the study area is described in detail in Hamao (2000).

The Black-browed Reed Warbler is a small (ca. 10 g), migrant passerine bird that is endemic to Northeast Asia, and is a summer resident of Japan (OSJ 2000). Males arrive at the study area from late May to mid-July and attract females by singing long, complex songs (Ueda & Yamaoka 1998; Hamao 2000). Females arrive at the site from early June to mid-July, and soon settle in the males' territories. Females build nests alone, taking widely varying periods to complete the nests (Hamao 2001). The modal clutch size is five. Although a female can produce fledglings twice in a breeding season, it is very rare. During one breeding season, 25% of the males acquired two, or rarely three, females, 56% acquired one female, and 19% remained solitary (Hamao, unpublished data).

2) Field observations

Birds were captured in mist nets soon after arrival, and were individually color-ringed. In some cases where females were building nests when I detected them, I marked the females after they laid their third egg to avoid making the females desert their nest. Using this marking method, no bird disappeared from the territory or deserted its nest. The study area was visited daily from late May to mid-August, except in cases of heavy rain. To monitor pair formation and nesting stage, I visited each of the territories daily or every two days, between sunrise (0440 ± 15 min during the study period) and 0800, and observed the behavior of marked birds from a 1.8-m-high stepladder.

Observations were made for 15–40 min in each territory. During my visits, I also inspected the nest contents. If all the eggs or nestlings in a nest disappeared, I assumed that it was due to predation.

The nest predation rate was based on observations of all nesting attempts that were identified before egg-laying started. Sixty-five such nesting attempts were identified, including renesting by females within the original territory. Data on mate choice, whether a female formed a pair-bond with an unpaired male or with an already-mated male, were obtained for 49 females. Forty-eight breeding females were observed from the time they settled in their territories, or from the early stage of nest building. I also included in this data set one female (#91) that I found after her clutch was complete. When I found this female, another female (#90) was also nesting within the same territory, and the male was apparently solitary before he paired with female #90. Therefore, female #91 clearly paired with the male who had already mated with female #90.

If a female renested with the same mate after nest predation, I used the final nesting attempt as the result of her mate choice. If the first nesting failed during the incubation period and the next nesting produced fledglings, I assumed that the female had produced eggs that hatched.

3) Parental activities

To monitor the incubation and feeding to nestlings by parents, I recorded the birds that visited focal nests with a Sony CCD-G100 video camera and a Sony GV-100 video recorder. The video recording was made for 2.6 ± 0.2 h (mean ± SE, N=43). To investigate incubation behavior, I videotaped the nests 5.2 ± 0.7 days (N=13) after the last egg was laid, and to examine feeding behavior, I videotaped the nests 6.0 ± 0.3 days (N=30) after the first egg hatched. The individuals recorded in the videotapes were identified by their leg rings, and I checked to see whether they incubated eggs and fed nestlings.

To describe parental activities, I divided the broods into three categories according to the situation on the day the nests were videotaped. When there was one nest in a territory, the brood was called a monogamous brood. When there were two nesting attempts within a territory, the brood at the more advanced nesting stage was assumed to be the primary brood and the one at the less advanced nesting stage was assumed to be the secondary brood. This definition reduced the number of secondary broods that I could

videotape, because it was uncommon for both broods of polygynously mated females to survive until the day I made video recordings, due to the high predation rate (see results). The time spent incubating by each parent was measured for nine monogamous, two primary, and two secondary broods. The share of feeding by parents was based on data obtained from 19 monogamous, eight primary, and three secondary broods. The nestling age at the time of video recording did not vary among the three brood categories (monogamous: 5.9 ± 0.3 days (mean \pm SE), primary: 5.6 ± 0.5 , secondary: 7.0 ± 1.2 ; Kruskal-Wallis test, $H=1.36$, $P=0.51$). The number of nestlings in a nest also did not vary among the categories (monogamous: 3.6 ± 0.2 , primary: 4.1 ± 0.3 , secondary: 4.0 ± 0.6 ; $H=2.57$, $P=0.28$).

To describe relation between mating and hatching order, I divided the broods into three categories by the same way according to the situation on the day the eggs hatched.

4) Statistical analyses

I compared the feeding behavior of different pairs in three brood categories: monogamous, primary, and secondary broods. Since the variance among the categories was unequal, I performed the robust rank-order test (Siegel & Castellan 1988) corrected by the sequential Bonferroni method (Rice 1989). All the statistical tests were two-tailed. Values are presented as means \pm SE.

RESULTS

1) Male parental care

Males seldom incubated eggs, irrespective of the brood status. Males did not participate in incubating primary or secondary broods. They incubated only three of nine monogamous broods, and the time that they spent incubating (3.6 ± 1.2 min h^{-1} , $N=3$) was much shorter than that by their mates (31.5 ± 2.0 min h^{-1} , $N=3$).

The frequency of male food delivery varied between the monogamous, primary, and secondary broods (Fig. 1a). Males never fed the secondary broods. Male feeding frequency differed significantly between monogamous and secondary broods ($\hat{U}=\infty$, $P<0.005$). Male feeding frequency also differed between primary and secondary broods, but the difference was not significant ($\hat{U}=5.72$, $0.05<P<0.10$).

The frequency of female food delivery did not differ significantly between any pairs in the three brood

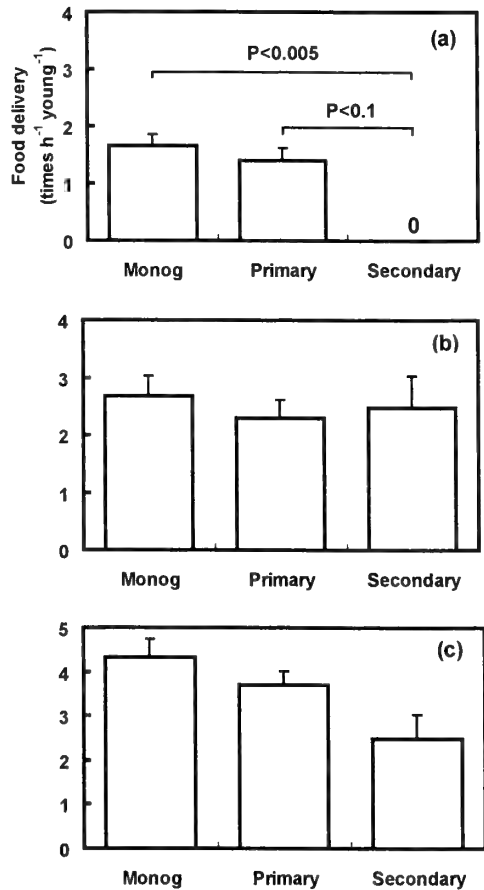


Fig. 1. Feeding frequency by the male (a), female (b), and both parents (c). The lines on the bars indicate the SE. The data were obtained from 19 monogamous, eight primary, and three secondary broods.

categories (all $P>0.2$; Fig. 1b). Therefore, the frequency with which both parents fed secondary broods was slightly lower than the frequency with which both parents fed monogamous and primary broods (Fig. 1c), but the differences between any pair of the three brood categories were not significant (all $P>0.1$).

2) Nest predation

Of 65 breeding attempts, 35 failed because of nest predation. Five of the nests were deserted by both parents. Two of the nests were destroyed when farmers cut the grass supporting the nests. Consequently, 23 nests produced fledglings. Excluding the two cases of artificial destruction, 56% of the nests ($N=63$) were preyed upon in the study area.

3) Relation between mating and hatching order

Thirty-five females paired with unpaired males,

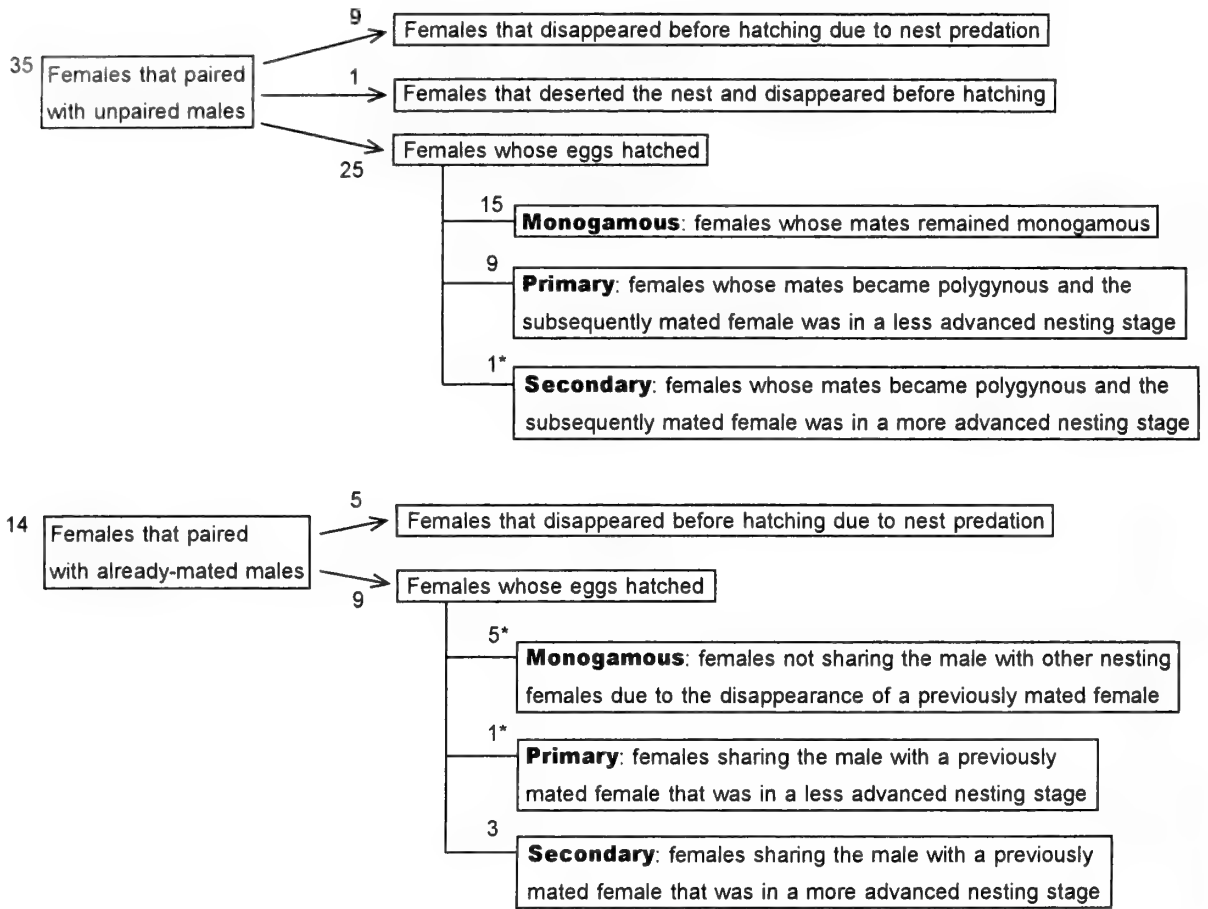


Fig. 2. Relationship between female mate choice and their status at egg-hatching. The figures are the numbers of females. The causes of the status changes labeled with asterisks are explained in Fig. 3.

and 10 (29%) of them disappeared from the territories before egg-hatching, due to nest predation (nine cases) or nest desertion (one case; Fig. 2). Therefore, 25 (71%) of the females that paired with unpaired males produced eggs that hatched. When the eggs hatched, the mates of 15 females remained monogamous (Fig. 2), while the mates of 10 females became polygynous. In the cases of polygyny, nine females were the mothers of primary broods at egg-hatching; i.e. the subsequently mated females were at a less advanced nesting stage (Fig. 2). However, one female became the mother of a secondary brood; i.e. the subsequently mated female was at a more advanced nesting stage (Fig. 2). This inversion in the order of the nesting cycles of the polygynously mated females occurred because the previously mated female built a nest three times before egg-laying, which prolonged her pre-laying period, and by the fact that her clutch was larger than that of the subsequently mated female, which also delayed the start of incubation (Fig.

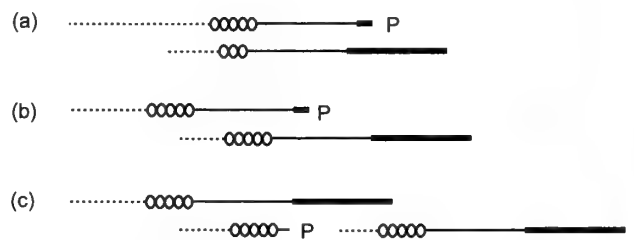


Fig. 3. Causes and patterns of change in female status. Broken lines: pre-laying, open circles: egg-laying, thin lines: incubation, thick lines: nestling, P: nest predation. A prolonged pre-laying period of a previously mated female also changed the status of the previously mated female (a). Nest predation of a previously mated female (b) and a subsequently mated female (c) also changed the status of the subsequently mated females. See text for details.

3a). Therefore, 69% (24/35) of the females that paired with unpaired males became the mothers of monogamous or primary broods at egg-hatching.

By contrast, 14 females paired with already-mated

males, and five (36%) of them disappeared from the territories before egg-hatching, due to nest predation (Fig. 2). Therefore, nine (64%) of the females that paired with already-mated males produced eggs that hatched. At egg-hatching, five females became the mothers of monogamous broods (Fig. 2), because the previously mated females had disappeared due to nest predation (four cases; Fig. 3b), or because renesting of the subsequently mated female due to predation delayed her egg-hatching, and the previously mated female and her fledglings disappeared in this interval (one case; Fig. 3c). One subsequently mated female became the mother of a primary brood because of the prolonged pre-laying period of the previously mated female (Fig. 3a). Furthermore, her brood became a monogamous brood during the nestling-rearing period, because the previously mated female's nest was preyed upon (Fig. 3a). Three females that paired with already-mated males became the mothers of secondary broods, so their status did not change throughout the nesting period. Therefore, 43% (6/14) of the females that paired with already-mated males became the mothers of monogamous or primary broods at egg-hatching. This proportion (6/14) did not differ significantly from the proportion of females (24/35) that paired with unpaired males ($\chi^2=2.79$, $df=1$, $P=0.10$).

DISCUSSION

Male Black-browed Reed Warblers did not feed later-hatched broods. This can be a potential cost when a female chooses an already-mated male as her mate. In some cases, however, female status changed between the time of pair formation and nestling-rearing. In this discussion, I exclude the status change from a monogamous to a primary brood, which occurs when the mate of a female succeeds in mating polygynously, because it does not affect male parental assistance to the female. With one exception, in which the nesting cycle of a polygynously mated female became inverted (Fig. 3a), any change in female status was caused by nest predation. When a previously mated female failed in her breeding attempt and disappeared from a territory, the subsequently mated female acquired monogamous status (Fig. 3b). This type of status change has been pointed out previously (Temrin & Jakobsson 1988; Urano 1990). Temrin and Jakobsson (1988) reported that almost half of the subsequently mated females of the Wood Warbler *Phylloscopus sibilatrix* had exclusive

male assistance because the nests of the previously mated females were preyed upon. I found another type of female status change: renesting of a subsequently mated female due to nest predation delayed her nesting cycle and resulted in her gaining monogamous status at egg-hatching (Fig. 3c).

The proportion of females acquiring monogamous or primary status at egg-hatching was higher for females that paired with unpaired males than it was for females that paired with already-mated males, although the difference was not significant. Therefore, although female Black-browed Reed Warblers will not necessarily receive male parental assistance more readily when they pair with already-mated males, nest predation allowed 43% of the females that chose already-mated males as their mates to receive male assistance. This suggests that nest predation reduces the cost of polygynous mating. If females incur a cost due to time constraints, for example, when they choose males, a female might pair with an already-mated male.

It is worth noting that when more than half of all nests were preyed upon, 69% of the females that paired with unpaired males and 43% of the females that paired with already-mated males acquired the status of the mothers of assisted broods. These proportions indicate the extent of the effect of nest predation on the cost of polygyny in this reed warbler population.

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ORIGINAL ARTICLE

Seed dispersal agents of two *Ficus* species in a disturbed tropical forestKelvin S.-H. PEH^{1,2,#} and Fong Lin CHONG¹¹ Department of Biological Sciences, National University of Singapore, Blk S2, 14 Science Drive 4, Singapore 117543, Republic of Singapore² Swedish Biodiversity Centre, CBM, Box 7007, 750 07 Uppsala, SwedenORNITHOLOGICAL
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Abstract Observations were carried out at the Bukit Timah Nature Reserve, Singapore on two species of the keystone genus, *Ficus fistulosa* and *F. grossularoides*. This study shows that the two species of different morphological characteristics (e.g. plant height, fruit colour and size) attracted different assemblage of avian frugivores. The frequency of visits by the avian frugivores was significantly different between the two *Ficus* species. The fig-eating frugivore communities feeding on both *Ficus* species seemed to be comparatively depauperate and a substantial number of members were the non-obligate (i.e. routine) avian frugivores. Mammalian frugivory was also observed. The mean number of feedings at *F. grossularoides* might not correlate with body size of the avian frugivores. Such information may aid the forest conservation and management of the nature reserve and future attempts at forest restoration.

Key words Biodiversity, Conservation, *Ficus*, Frugivory, Fig-disperser declines, Seed dispersal

Ficus is one of the largest genus with approximately 350 species in Southeast Asia (Corner 1965). It is widely considered as a keystone mutualist for many vertebrates in the tropical rain forest (e.g. Janzen 1979). Being abundant and always available throughout the year, figs constitute an important diet for many frugivorous animals when other food resources (e.g. insects) are scarce (Leighton and Leighton 1983). It comprises the most important class of plant resources as Terborgh (1986) has shown that the species that feed on the figs constitute about 40% of the animal biomass at Cocha cashu, Peru. Lambert and Marshall (1991) identified the characteristics, which make figs the most important keystone plant resources: their large crop sizes, relatively short fruiting intervals, intra-crown synchrony of fruit ripening and intra-population asynchrony.

The ecological and evolutionary importance of frugivores as seed dispersers in tropical rain forest is well studied (e.g., Estranda and Coates-Estranda 1986; Fleming 1986). The mutualistic relationships between *Ficus* and frugivores are also well known.

Ficus is heavily dependent on the frugivores to disperse their seeds (Lambert 1989; Lambert 1991). Seed dispersal by animals ensures the long-term survival of many *Ficus* species. Such ecological processes provided by the frugivores may also determine the *Ficus* species and genetic composition in the disturbed landscapes (Corlett 1995; Hamilton 1999). Thus the patterns of visit by frugivores may influence the succession in disturbed areas such as the forest edge or gaps. On the other hand, the presence of fruiting trees in the disturbed landscapes may maintain the frugivorous faunal communities in these areas (da Silva et al. 1996; Restrepo et al. 1999). Understanding such ecological processes is essential for the conservation of biodiversity and restoration of the disturbed landscapes.

In this study we attempted to fill the gaps in knowledge on the fig-eating frugivore assemblage in a disturbed forest habitat. First, we recorded the composition of diurnal vertebrate assembly, feeding on the figs of the two keystone pioneer *Ficus* species, *F. fistulosa* and *F. grossularoides* in a highly isolated, disturbed forest reserve. We compared the species assemblage and visitation pattern in term of frequency and number of fruit consumption, feeding guild and

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feeding method of frugivores between the two *Ficus* species. The comparison of the feeding guild and fruit consumption of the visiting frugivores for each *Ficus* species could provide information on their fruit usage and this relates to the importance of figs as a food source. We determined if there was a relation between the frugivore's body size and the number of figs eaten because it is always assumed that the larger frugivores tend to be more efficient fig dispersers as they consume more figs (e.g. Shanahan et al. 2000). We indirectly examined the relative importance of the observed frugivores for both *Ficus* species based on literature reviews (e.g. Corlett 1998; Shanahan et al. 2000). Lastly, we reviewed the conservation status of resident fig-eating birds of the reserve.

METHODS

1) Study site

The study was carried out between 20 January and 24 March 1999 at the Bukit Timah Nature Reserve (hereafter Bukit Timah) in the mainland of Singapore (1°20'N 103°50'E), which situated in a typical equatorial climate. Bukit Timah is a small, isolated forest fragment with the surrounding matrix of urban areas. The 71 ha nature reserve comprises primary hill Dipterocarp forest, which has never been logged, and secondary forest patches of various ages (Corlett 1990). Despite its small size and high human disturbance, Bukit Timah harbours a high floral diversity with more than 800 species of native plants (Corlett 1990). It is also the last primary forest remnant in Singapore where native mammals, birds, reptiles and invertebrates can still be found. The area surveyed was a stretch of forest of secondary nature in the more disturbed part of the reserve.

2) Study subjects

We chose *Ficus fistulosa* and *F. grossularoides* for this study primarily because of their relative abundance. Both members of the *Ficus* are pioneer species, commonly found in the secondary patches of Bukit Timah. They are different morphologically in terms of plant height, fruit size, fruit colour and probably also in their palatability and inherent nutrition. *F. fistulosa* is the taller of the two, reaching a height of 9 m. Its fruits are borne in clusters on woody knobs that line the trunk and main branches. The fruit, of the average diameter of 2.5 cm, are green with white dots, ripening to pale yellow or greenish yellow. *F. grossularoides* is a shrub-like or small tree that

reached a maximum of 3 m. Its fruits have an average diameter of 1.25 cm. Those are sessile, round and are mostly on twigs just below the leaves. Those ripen from yellow to brownish ochre to dark red. Descriptions of the two *Ficus* species are derived from Ng (1978).

3) Focal observations and statistical analyses

We conducted an observation for 12 days between 0700 h and 1000 h when the frugivores are most actively feeding in the morning. Different fruiting trees of both *Ficus fistulosa* and *F. grossularoides* were sampled for each morning session. Thus 12 trees with a total of 18 h of observation were performed for each *Ficus* species. For every session, we chose one fruiting tree of each *Ficus* species, of which at least half of their crown visible from the ground, for focal watch. The observations were carried out in 15 min blocks that alternated between the two species. Binoculars (8×30) were used to aid in identification of the feeding frugivores. Identification of the avian and mammalian frugivores followed King et al. (1989) and Lekagul and McNeely (1988) respectively.

Frugivores foraging in the fruiting *Ficus* trees were recorded and grouped accordingly to their feeding guilds: animals that are obligate frugivores feed mainly on fruits and routine frugivores have a wide range of mixed diet. Foraging habits of the frugivores in the fruiting *Ficus* were also observed and classified into three feeding methods following Trainer and Mill (1984): species that are "swallowers" took the figs as a whole, "marshers" that squashed the figs in the beaks before swallowing the whole or most of the fruit, and "biters" that pecked at the fruit, feeding on the figs in small bits.

We noted the number of fruit eaten by the visiting frugivores. The taking of a whole fruit or any removal of the fruit in small section was counted as a feeding. When it was not obvious if the animal had fed on some fruit, the head-pecking movements were counted as well. We used Spearman-ranked correlation test to determine if there was any relation between the mean number of figs eaten by the "swallowers" and their body sizes. Body sizes of the frugivores were obtained from Robson (2000). All data are analysed using Statistical Analysis System (SAS). Invertebrates, like ants and other insects, were not included in this study. Another important group of frugivores, fruit bats, was also not dealt with.

4) Fig-eating bird assemblage

We compiled a checklist of forest resident fig-eating birds of Bukit Timah, from pre-1940 to 1991, based on literature research (e.g. Lim 1992; Shanahan et al. 2000) and personal observations. The conservation status of these fig-eating frugivores in Bukit Timah was reviewed according to Lim (1992). The quality of the fig seed dispersers was difficult to judge and was based on a review paper by Corlett (1998). The nomenclature of avian and mammalian frugivores followed Inskipp et al. (1990) and Corbet and Hill (1991), respectively.

RESULTS

1) Birds

A total of 15 bird species were spotted feeding on figs of both *Ficus* species (Table 1). Four species of birds were observed feeding on figs of *F. fistulosa* whereas 14 species were seen on *F. grossularoides*. We observed eight individuals belonging to three resident and one introduced species on *F. fistulosa*. The most common species seen feeding on the figs of *F. fistulosa* was the Pink-necked Pigeons. We found 34 individuals belonging to 13 resident and one migrant

species feeding on the figs of *F. grossularoides*. The Pink-necked Pigeons were the most common frugivores for *F. grossularoides*, followed by the Yellow-vented Bulbul and White-vented Myna. The common species that fed on both *Ficus* were the Pink-necked Pigeons, Black-naped Orioles and Asian Glossy Starlings. More species of avian frugivores were observed feeding on *F. grossularoides* than on *F. fistulosa* ($\chi^2=6.20$, $P<0.05$). Similarly, more individuals were seen feeding on *F. grossularoides* than on *F. fistulosa* ($\chi^2=16.12$, $P<0.01$).

The average number of feedings by all avian "biter" species for *F. fistulosa* ranged from three to five pecks per visitation (Table 1). The only "swallower" for *F. fistulosa*, the Great Hornbill, was observed to consume eight figs during its one-timed visitation. The biters for *F. grossularoides* comprised three species, which had an average of two to six mean feedings per visitation. The average number of feedings for *F. grossularoides* by the "swallowers" species (12 species) ranged from two to nine figs per visit. For *F. grossularoides*, one Asian Fairy Bluebird was observed to swallow the most number of fruits, a total of 9 figs during its visitation.

Table 1. List of frugivores observed feeding on *Ficus fistulosa* and *F. grossularoides* between 20 January and 24 March 1999. Terminology for feeding methods follows Trainer & Will (1984). X indicates no data available.

Species	Feeding guilds	<i>Ficus fistulosa</i>			<i>Ficus grossularoides</i>		
		Feeding Methods	N visits	Mean N feedings	Feeding Methods	N visits	Mean N feedings
Birds							
Great Hornbill <i>Buceros bicornis</i>	Routine	Swallower	1	8.0			
Red-crowned Barbet <i>Megalaima rafflesii</i>	Obligate				Swallower	1	5.0
Coppersmith Barbet <i>Megalaima haemacephala</i>	Obligate				Swallower	1	2.0
Pink-necked Pigeon <i>Treron vernans</i>	Obligate	Biter	4	5.0	Swallower	9	3.5
House Crow <i>Corvus splendens</i>	Routine				Swallower	1	X
Scarlet-backed Flowerpecker <i>Dicaeum cruentatum</i>	Routine				Biter	1	6.0
Orange-bellied Flowerpecker <i>Dicaeum trigonostigma</i>	Routine				Biter	1	2.5
Asian Fairy Bluebird <i>Irena puella</i>	Obligate				Swallower	1	9.0
Black-naped Oriole <i>Oriolus chinensis</i>	Routine	Biter	2	3.5	Swallower	2	6.0
Yellow-vented Bulbul <i>Pycnonotus goiavier</i>	Routine				Swallower	7	3.8
Olive-winged Bulbul <i>Pycnonotus plumosus</i>	Routine				Swallower	1	7.0
White-vented Myna <i>Acridotheres javanicus</i>	Routine				Swallower	5	3.4
Asian Glossy Starling <i>Aplonis panayensis</i>	Obligate	Biter	1	3.0	Swallower	2	4.0
Short-tailed Babbler <i>Trichastoma malaccense</i>	Routine				Biter	1	2.0
Eye-browed Thrush <i>Turdus obscurus</i>	Routine				Swallower	1	X
Mammals							
Common Treeshrew <i>Tupaia glis</i>	Routine	Biter	1	X			
Long-tailed Macaque <i>Macaca fascicularis</i>	Obligate	Marshes	6	X			
Plantain Squirrel <i>Callosciurus notatus</i>	Routine	Biter	5	2.8	Biter	3	3.0

2) Mammals

Three species of mammals were found to be feeding on the figs of one or both *Ficus* species (Table 1). They were the Common Treeshrews, Long-tailed Macaques and Plantain Squirrels. We observed 12 individuals belonging to three mammalian species feeding on the figs of *F. fistulosa* but recorded only three Plantain Squirrels feeding on *F. grossularoides*. Thus, more individuals of mammals were observed feeding on *F. fistulosa* than on *F. grossularoides* ($\chi^2=5.46$, $P<0.05$). The most common mammal eating the figs of *F. fistulosa* was the Long-tailed Macaques.

The average number of feedings by the Plantain Squirrels for *F. fistulosa* and *F. grossularoides* are 2.8 and three per visitation, respectively (Table 1). The data for other species was unable to obtain because poor visibility hampered the observation.

3) Feeding guilds, Foraging methods and Body sizes

The relative abundance of non-obligate (i.e. routine) frugivore among the vertebrate assembly was substantial for both *Ficus* species (Fig. 1). Only three species, which comprised 11 individuals, were considered as obligate frugivores among the species assemblage for *F. fistulosa*. The obligate frugivores feeding at *F. grossularoides* included four species of a total of 14 individuals. The numbers of obligate frugivores (including mammals) between both *Ficus* species are not significantly different ($\chi^2=0.4$, $P>0.01$). However, more obligate avian frugivores were observed feeding at *F. grossularoides* than at *F. fistulosa* ($\chi^2=4.31$, $P<0.05$).

More "swallowers" were observed feeding on *F. grossularoides* whereas the consumers for *F. fistulosa* were mostly "biters" (Fig. 2). There was an absence of "marshers" on *F. grossularoides*. For the avian frugivores that swallowed figs of *F. grossularoides*, we found that there was no correlation between the number of fig eaten and their body sizes (Spearman-ranked correlation=0.373, $P>0.05$).

4) Fig-eating bird assemblage

46.2% of the 65 resident avian fig-eating species from 17 families recorded since pre-1940 still persist in Bukit Timah. Of the remaining 30 species, 66.7% are considered to be of high quality fig-seed dispersing (HQFD) species which are more efficient at seed dispersal. However only nine species are HQFD forest specialists and all of them are classified locally as

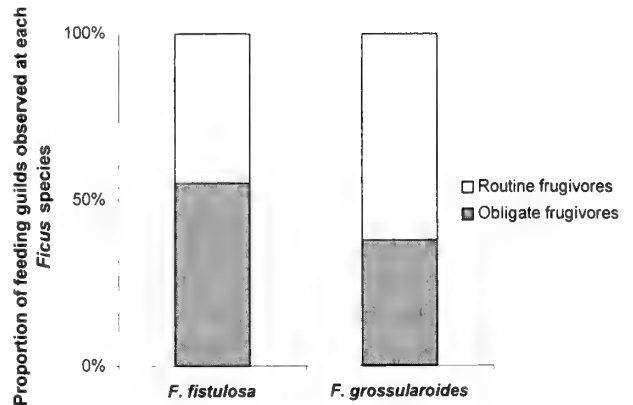


Fig. 1. Proportion of feeding guilds observed at both *Ficus fistulosa* and *F. grossularoides* based on the number of individuals observed. Routine frugivores are species that have a wide range of mixed diet whereas obligate frugivores feed mainly on fruits.

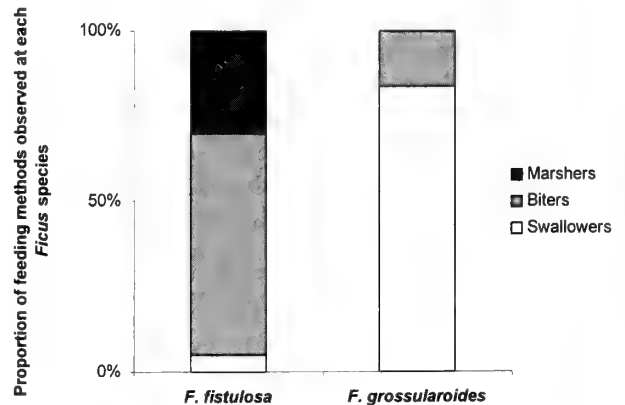


Fig. 2. Proportion of feeding methods observed at both *Ficus fistulosa* and *F. grossularoides*, based on the number of individuals observed. Definitions for foraging methods follow Trainer and Will (1984).

threatened species (Table 2). The more important avian fig-eating families at Bukit Timah in term of the number of genera and species eating figs are Pycnonotidae, Irenidae, Corvidae, Nectariniidae, Cuculidae and Lybiidae. We observed 10% of the total HQFD species assemblage feeding on figs of *F. fistulosa* and 4% of that on *F. grossularoides* (excluding winter migrants, reintroduced and non-native species).

DISCUSSION

Comparison between *F. fistulosa* and *F. grossularoides* shows the difference in frugivore diversity. Both species exhibit different characteristics, which attracted different assemblage of diurnal frugivores.

Table 2. Contributions of families to total number of high quality fig dispersing (HQFD) species in Bukit Timah from pre-1940 to 1991. The quality of the fig dispersers was based on Corlett (1998). Migrants and non-native species were not included.

Families	Total fig dispersers (N)	Extinct species (N)	Extant HQFD (N)	HQFD forest specialists (N)	Threatened HQFD forest specialists (N)	Proportion of HQFD in relation to total extant fig dispersing species (%)
Phasianidae	2	2	0	0	0	0
Lybiidae	6	4	2	1	1	6.7
Picidae	2	1	0	0	0	0
Bucerotidae	3	3	0	0	0	0
Dacelonidae	1	1	0	0	0	0
Trogonidae	1	1	0	0	0	0
Cuculidae	2	0	2	1	1	6.7
Psittacidae	3	0	0	0	0	0
Columbidae	6	3	0	0	0	0
Rallidae	1	0	0	0	0	0
Corvidae	9	5	3	0	0	10.0
Eurylaimidae	4	4	0	0	0	0
Irenidae	4	0	4	4	4	13.3
Nectariniidae	8	5	3	1	1	10.0
Pycnonotidae	10	6	4	2	2	13.3
Sturnidae	2	0	2	0	0	0
Sylviidae	1	0	0	0	0	0

The potential primary dispersal agents for *F. fistulosa* are mainly terrestrial mammals and bats (Lambert 1991). Its figs are too large for most avian frugivores to swallow as a whole. Although the fruits of *F. fistulosa* do not show any of the typical bird-dispersal syndromes described by van der Pijl (1972), they caught the attention of some relatively larger birds such as the Great Hornbill and Pink-necked Pigeons and also 10% of the total HQFD species assemblage at Bukit Timah. This showed that *F. fistulosa* fits into the description for tropical *Ficus* species associated with generalist nature of the disperser assemblage. The contribution of individual frugivore species varied considerably. The HQFD species observed feeding in *F. fistulosa* were the Black-naped Oriole, Asian Glossy Starling and Long-tailed Macaque. Since half of the recorded avian visits were pink-necked pigeons, this seed predator exhibited a pattern of dominance in avian fig-eating assemblage to *F. fistulosa*.

On the other hand, *F. grossularoides* were visited by a wider range of fig-eating birds even though Lambert (1989) reported that there was no bird feeding on the figs of *F. grossularoides* at Kuala Lompat, Malaysia. Although *F. grossularoides* exhibits typical bird dispersing qualities in fruit size, colour and asynchrony in ripening, its figs are also readily consumed

by the Short-nosed Fruit Bats, *Cynopterus* spp. (Ling Ong, pers.com). Most of the avian frugivores swallowed the figs except the smallest flowerpeckers that pecked the fleshy tissues of the figs. The HQFD species observed on *F. grossularoides* were the Red-crowned Barbet, Coppersmith Barbet, Scarlet-backed Flowerpecker, Orange-bellied Flowerpecker, Asian Fairy Bluebird, Black-naped Oriole, Yellow-vented Bulbul, Olive-winged Bulbul and Asian Glossy Starling. The Pink-necked Pigeons and Yellow-vented Bulbuls dominated the fig-eating assemblage. Most of these species are the smaller frugivores, which are not obligate fig-eaters. Nevertheless, these small generalists are important for the fig seed dispersal as our results suggested that the number of figs eaten might not correlate with body sizes of the birds.

Only nine avian HQFD species at Bukit Timah are forest specialists that frequent in relatively undisturbed part of the reserve, and all of them are classified as locally threatened species. They are the Red-crowned Barbet, Drongo Cuckoo, Blue-winged Leafbird, Lesser Green Leafbird, Greater Green Leafbird, Asian Fairy Bluebird, Yellow-vented Flowerpecker, Red-eyed Bulbul and Cream-vented Bulbul. The declines of the fig-eating frugivores at Bukit Timah since 1800s no doubt limited the number of species

feeding on both *F. fistulosa* and *F. grossularoides*. The absence of more important fig-seed dispersers at Bukit Timah may lead to a dominance of small generalist (routine) frugivores that are more tolerant to fragmentation and able to switch diets opportunistically in their altered landscapes (Table 1; Fig. 2). The only avian HQFD forest specialists contributed to the recorded visits were the Red-crowned Barbet and Asian Fairy Bluebird. The loss of HQFD species in biotic communities may have an irreversible effect on the stability, functioning and sustainability of an ecosystem (Tilman 1997). Bukit Timah serves as a forecast of what may happen to fig-eating frugivores as a result of habitat disturbance and fragmentation. It also reflects a trend of global declines for individual species and populations of fig-eating frugivores. Excluding fig-eating reptiles and fishes, about 18% of all bird and mammalian species known to eat figs are either at risk or near threatened at a global level (Peh K.S.-H., unpublished data).

Although habitat destruction and fragmentation have been identified by many studies as root causes of the current global biodiversity crisis and conservation problems (e.g. Turner 1996; Debinski & Holt 2000), serious threats faced by fig-eating frugivores include disturbance of roost sites, poaching, introduction of alien predators, harmful effects of environmental pollution and unpredictable natural disturbances such as hurricanes. All cases of threats have the potential to result in the local loss of fig-eating species. Efforts to address the issues of fig-eating frugivores declines in disturbed habitats are very much needed. Information on the interaction patterns among fig-seed dispersers and *Ficus* in rain forests with respect to community structure, degree of generalization or specialization of interactions, and ecosystems health may be vital for forest conservation and management of small reserves. Such knowledge may also aid in any future attempts in rain forest restoration.

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SHORT COMMUNICATION

Ants found in scats and pellets taken from the nests of the Japanese Wryneck *Jynx torquilla japonica*

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The Japanese Wryneck *Jynx torquilla japonica* (Bonaparte 1850) is a subspecies of *J. torquilla* Linnaeus, 1758 (Ornithological Society of Japan 2000). *J. t. japonica* has been recorded breeding only in the southern part of the Kurile Islands, Hokkaido, and the northern part of Honshu, Japan (Fujii 1990; Satoh et al. 1996; Ornithological Society of Japan 2000). Short (1982) and Winkler and Christie (2002) suggested that the subspecies *J. t. japonica* is synonymous with *J. t. torquilla*. Ecological information is needed to clarify the taxonomic status of the Japanese population.

Ants (Formicidae) are considered one of the major food items for *J. t. japonica* (Yamashina 1941; Kiyosu 1965), and there have been a few reports about ants as prey. Kosugi (1989) observed that chicks were fed larvae and adult ants on Rishiri Island, northern Hokkaido. Satoh et al. (1996) also reported that ant eggs and pupae were given as food, and Murai and Higuchi (1991) observed ant pupae being carried into a *J. t. japonica* nest. In his book, Kiyosu (1965) described ant adults and larvae as being a favored food item of *J. t. japonica*, and Fujii (1990) reported that ant pupae are the most common food for *J. t. japonica* chicks.

Although the ant species recorded by Kiyosu (1965) were *Lasius japonicus*, and Kuro-ari (possibly *Lasius nipponensis* or *Camponotus (Myrmamblys) itoi*) and that recorded in Fujii (1990) was probably *Formica sanguinea*, the ant species in the reports by Kosugi (1989), Satoh et al. (1996), and Murai and Higuchi (1991) were unidentified. There has not been sufficient analysis of the ants eaten by *Jynx torquilla*

japonica. Detailed identification of the prey ant species will help to clarify the bird's food habits.

In this paper we analyzed ant remains recovered from scats and pellets found in post-breeding nests of *Jynx torquilla japonica* in Tokachi, Hokkaido, Japan. This is the first detailed report on prey species for *J. t. japonica*. We also discuss the food habits of *J. t. japonica*.

MATERIAL AND METHOD

Scats and pellets from four nests of *Jynx torquilla japonica* were analyzed. Sampling was done immediately after fledging, from June to August in 2002. Scats and pellets were collected using different methods: chips with adhesives (nests I and II), by hand from the bottom of cavities (nest III), or by hand from the bottom of a bird box (nest IV). Of the four sampling nests, I and II were in open land, and III and IV were in humid forests. For nests I, II, and III, *J. t. japonica* used cavities made by woodpeckers. Nest IV was in a bird box. Measuring the diameters of the entrances suggested that nests I and II were made by *Dendrocopos major*, and nest III by *D. minor*, according to Yamauchi et al. (1997). Table 1 shows sampling dates, and describes the nests and their environments. The scats and pellets were broken up in ethanol, and identifiable parts of ants were collected with the aid of a stereoscopic microscope. The parts of ants recovered from scats and pellets were treated as samples of each nest. Samples were fixed with 70% ethanol and mounted as dry specimens before identification (Fig. 2). The species in the samples were identified by comparing them with reference specimens collected in Hokkaido. The bodies of the reference specimens were dismembered (head,

Table 1. Sampling information of seats and pellets of the Japanese Wryneck *Jynx torquilla japonica*. Sampling dates, description of the nest surveyed, and the environments surrounding the nest sites are shown. The environments list dominant tree species.

Nest No.	Sampling date	Description of the nest	Nest site environment
I	2002.vii.31	A cavity in a tree <i>Fraxinus mandshurica</i> var. <i>japonica</i>	Grassland, adjoining the forest mainly consisting of <i>Salix</i> spp.
II	2002.viii.6	A cavity in a tree <i>Betula platyphylla</i> var. <i>japonica</i>	Row of <i>Betula platyphylla</i> var. <i>japonica</i> adjoining open land
III	2002.vii.15	A cavity in a tree <i>Alnus hirsuta</i>	Humid forest, mainly consisting of <i>Alnus hirsuta</i> and <i>Populus maximowiczii</i>
IV	2002.vii.16	A nest box	Humid forest, consisting of <i>Fraxinus mandshurica</i> var. <i>japonica</i> , <i>Ulmus davidiana</i> var. <i>japonica</i> , and <i>Alnus japonica</i>

Table 2. The ant species collected from four post-breeding nests of *Jynx torquilla japonica*. The appearance of each species are shown as + in each cell of the nest. If only one individual was collected, the caste name is given as a singular form. Developmental stages are given as adult (Ad) or cocoon (Co). Nesting habitats of each ant species are shown as four categories: in the soil of open lands (SO), in the soil of forests (SF), in woods of open lands (WO), and in woods of forests (WF).

Scientific name	Japanese name	Caste	Developmental stage	Breeding nest				Nesting habitat
				I	II	III	IV	
<i>Formica japonica</i>	Kuro-yama-ari	workers	Ad		+		+	SO
<i>Formica candida</i>	Tsuya-kuro-yama-ari	workers	Ad		+		+	SO
<i>Formica truncorum</i>	Kezune-aka-yama-ari	workers	Ad			+		SO
<i>Lasius (Lasius) japonicus</i>	Tobihiro-ke-ari	workers	Ad	+		+	+	SO, SF, WO, WF
<i>Lasius (Lasius) japonicus</i>	Tobihiro-ke-ari	queen	Ad			+		SO, SF, WO, WF
<i>Lasius (Lasius) japonicus</i>	Tobihiro-ke-ari	males and queens	Co			+		SO, SF, WO, WF
<i>Lasius (Lasius) sakagamii</i>	Kawara-ke-ari	workers	Ad			+	+	SO
<i>Lasius (Cautolasius) flavus</i>	Kiuro-ke-ari	workers	Ad		+	+	+	SO, SF
<i>Lasius (Dendrolasius) spathepus</i>	Kusa-ari-modoki	male	Ad		+			SF, WF
<i>Lasius</i> sp. A	Ke-ari-zoku	workers	Ad				+	unknown
<i>Lasius</i> sp. B	Ke-ari-zoku	queen	Ad		+			unknown
<i>Lasius</i> sp. C	Ke-ari-zoku	males and queens	Co				+	unknown
<i>Myrmica kotokui</i>	Shiwa-kushike-ari	workers	Ad			+		WF
<i>Myrmica jessensis</i>	Ezo-kushike-ari	workers	Ad		+	+	+	SO
<i>Pheidole fervida</i>	Azuma-oozu-ari	workers	Ad		+		+	SO

scapes, pedicels and flagella, mandibles, pronotum, meso-metathorax and propodeum, petiole, postpetiole (if present), gaster, coxae, femora, tibiae, and tarsi) before the comparison (Fig. 1). The Japanese names of the ants follow the Japanese Ant Database Group (2003) and The Myrmecological Society of Japan Editorial Committee (1988).

RESULTS

Table 2 shows the names of the species, castes, and developmental stages of the ants from each nest, and

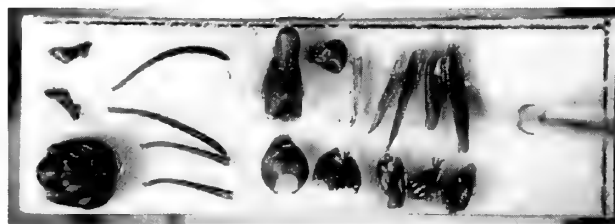


Fig. 1. Reference specimen (*Formica japonica*) that has been taken to pieces.

their nest habitats in Tokachi. A total of 13 ant species from four genera were found in the four nests of *J. t. japonica*. Ten of the 13 species were identified to species rank: *Formica japonica* (Fig. 2-J), *F. candida* (Fig. 2-K, P), *F. truncorum* (Fig. 2-A), *Lasius japonicus* (Fig. 2-B, F, O, S), *L. sakagamii* (Fig. 2-E, N), *L. spathepus* (Fig. 2-M), *L. flavus* (Fig. 2-C, G), *Myrmica kotokui* (Fig. 2-I), *M. jessensis* (Fig. 2-L), and *Pheidole fervida* (Fig. 2-H). The remaining three were identified to genus rank: belonging to the genus *Lasius*. Many cocoons of males and queens of *L. japonicus* were obtained from nest III, those of *Lasius* sp. C from nest IV, a queen of *L. japonicus* was found in nest III, and a queen of *L. sp.* B in nest II. *Lasius spathepus* from nest II was identified by a male petiole. There were common genera in the following nests: the genus *Lasius* in nests II, III, and IV, the genus *Formica* in nests II and IV, and the genus *Myrmica* in nests II, III, and IV.

We observed nest habitats in Obihiro for the 10 ant species identified to species rank. *Lasius japonicus*, *L. spathepus*, and *Myrmica kotokui* nest in wood, and the other seven species nest in the soil. *M. kotokui* and *L. spathepus* generally nest in forests, *L. japonicus* and *L. flavus* in both sparse forests and open land, and the remaining six species generally nest in open land.

DISCUSSION

In previous studies, only three ant species were reported as food items for *Jynx torquilla japonica* (Kiyosu 1965; Fujii 1990). In the present study, 13 species have been recognized, and nine of the records are new. Kiyosu (1965) writes that *J. t. japonica* forages in rotten parts of trees and on the ground, and Yamashina (1941) and Nakamura and Nakamura (1995) also state that the birds commonly forage on the ground in sparse forests. In the present study, seven species of the prey ants nest in the soil on open land in Tokachi. We found not only adult workers but also many cocoons from the reproductive castes among the bird scats and pellets. A forest species, *Lasius spathepus*, was found, but as the only finding was a male, it is likely that its capture occurred outside the ant's nest. Our results suggest that *J. t. japonica* generally forages on the ground, and takes adult ants and their pupae directly from nests in the soil. In addition, because many individuals of *Myrmica kotokui* were found, it is suggested that *J. t. japonica* also forages where ants make their nests among rot-

ten branches or wood on the ground. Because of our analysis of the food habits of *J. t. japonica*, it is probable that ant larvae are also one of the important food resources in the breeding season, although we did not find them in the scats and pellets.

Reports about the food preferences of the Eurasian Wryneck, *J. t. torquilla*, come mainly from Europe and Russia. In Europe, most of the food items consist of ants, *Lasius niger*, *L. alienus*, *L. emarginatus*, *L. flavus*, *Formica rufa*, *F. polyctena*, *F. fusca*, *F. cunicularia*, *F. rufibarbis*, *Myrmica lobicornis*, *M. sabuleti*, *M. scabrinodis*, *M. schencki*, *M. sulcinodis*, *M. rubra*, *Aphaenogaster subterranea*, *Leptothorax unifasciatus*, *Tetramorium caespitum*, and *Tapinoma erraticum* (Cramp 1985; Bitz & Rohe 1993), but other items are common in Russia: grasshoppers, aphids, beetles, craneflies, mayflies, and eggs of the Great Tit *Parus major* (Cramp 1985). Bitz and Rohe (1993) also reported from Germany that species belonging to the genus *Lasius* are the most common food items for *J. t. torquilla* through their analysis of 22013 food balls (Nahrungsballen). In our study, the food items from *J. t. japonica*'s scats and pellets consisted mostly of ants, and rarely included beetles or flies. *Lasius flavus* is contained as their food item for both *J. t. japonica* and *J. t. torquilla*. We also found that ant species belonging to the genera *Lasius*, *Formica*, and *Myrmica* are common food items for *J. t. japonica*, which is also the case with the European population. Our study of food habits supports a hypothesis of synonymy between *J. t. japonica* and *J. t. torquilla*.

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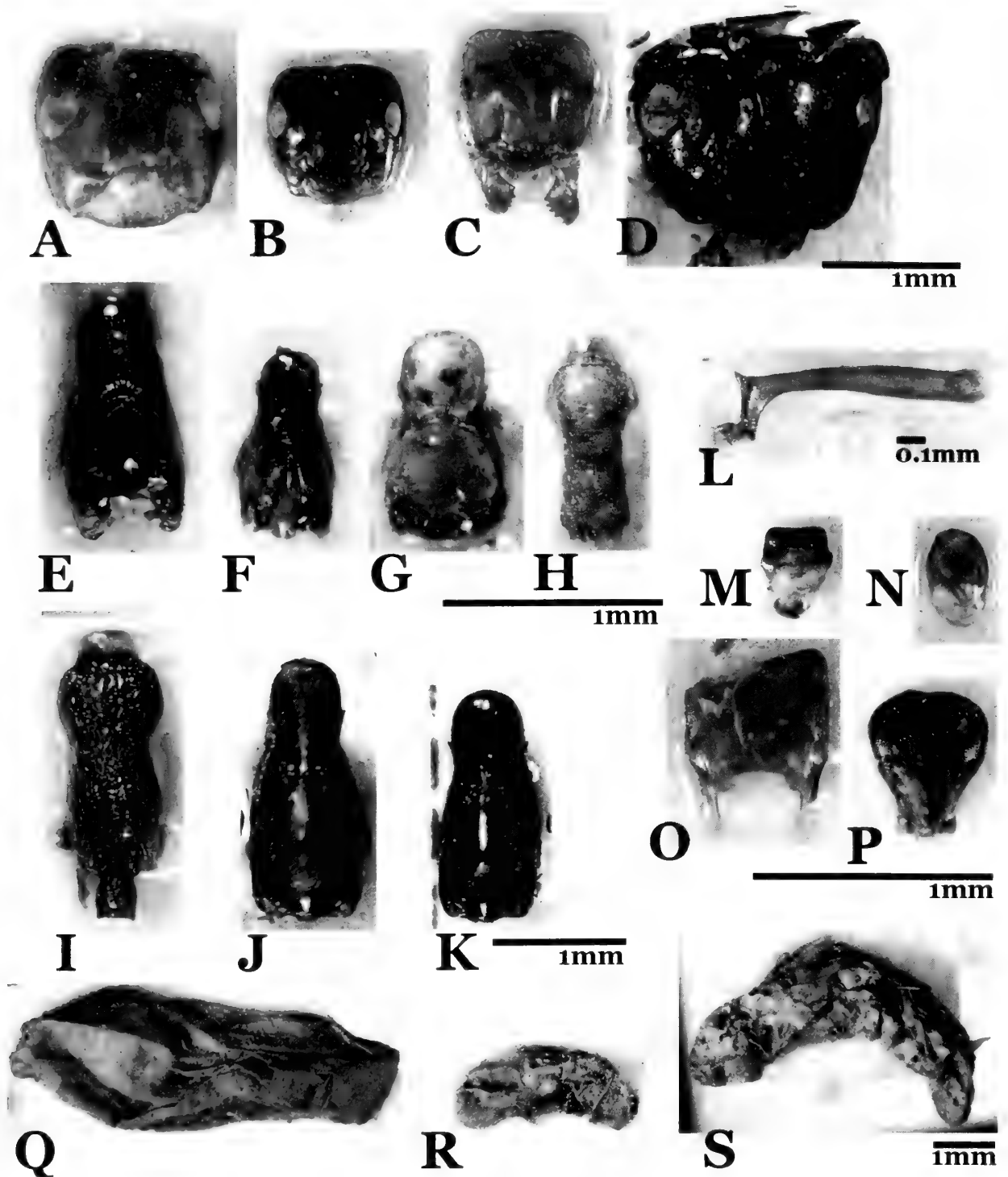


Fig. 2. Identifiable body parts of ants found in scats and pellets from *J. t. japonica*. F: from nest I; D, G, H, L, M: from nest II; A–C, E, I, N, O, S: from nest III; J, K, P–R: from nest IV. A: *Formica truncorum*; B, F, O, S: *Lasius japonicus*; C, G: *Lasius flavus*; D: *Lasius* sp. B; E, N: *Lasius sakagami*; H: *Pheidole fervida*; I: *Myrmica kotokui*; J: *Formica japonica*; K, P: *Formica candida*; L: *Myrmica jessensis*; M: *Lasius spathepus*; Q, R: *Lasius* sp. C. A–C, E–L, N, P: worker; D, O: queen; M: male; Q–S: cocoon. A–D: head; E–H, J, K: meso-metathorax and propodeum; I: Mesosoma and petiole; L: scape; M–P: petiole.

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SHORT COMMUNICATION

Interspecific learning by the Ogasawara Islands Honeyeater *Apalopteron familiare* from the Japanese White-eye *Zosterops japonicus* on Hahajima, the Bonin Islands, southern Japan

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The Ogasawara Islands Honeyeater *Apalopteron familiare* is endemic to the Bonin Islands, and classified as vulnerable by BirdLife International (2001). The Japanese White-eye *Zosterops japonicus* was introduced there in the early 1900s as a cage bird (Momiya 1930), and is now one of the most common bird species on the archipelago (Suzuki 1991). The former prefers primary forests and the latter prefers open habitats (Kawakami & Higuchi in press). The two species are similar in size and foraging habits, and their distributions overlap greatly in secondary forests, which constitute a large area of Hahajima (Kawakami & Higuchi in press).

In various studies, introduced species are considered to increase the costs or decrease the benefits to native species (e.g. Long 1981, Eguchi & Amano 1999), and the Japanese White-eye is considered to have that kind of impact on the Ogasawara Islands Honeyeater (Morioka & Sakane 1978, Department of Labor and Economy of Tokyo Metropolitan Government 1985). But in this case, there is also a possibility that the Japanese White-eye benefits the Ogasawara Islands Honeyeater.

The Japanese White-eye has a wide home range and high mobility (Kawakami & Higuchi unpublished data), and often feeds on a variety of insects and fruits. Many of the fruits are introduced species such as *Carica papaya* and *Morus australis* (Kawakami & Higuchi 2003). Conversely, the Ogasawara Islands Honeyeater has a smaller home range and its diet consists mainly of native foods such as small arthropods (Kawakami & Higuchi 2003). How-

ever, this species also forages on introduced fruits, and it is possible that Ogasawara Islands Honeyeaters have learned to eat such unfamiliar foods from Japanese White-eyes.

Laboratory experiments with the House Sparrow *Passer domesticus* (Fryday & Greig 1994), the Red Junglefowl *Gallus gallus* (McQuoid & Galef 1994), and the Black-capped Chickadee *Parus arcticus* (Sherry and Galef 1990), showed that demonstrators that ate unfamiliar food influenced the food preferences of observers. The same phenomenon might be occurring with the two bird species in the Bonin Islands. The purpose of the present paper is to show whether interspecific learning exists between the two species.

In order to find out if the birds were learning from each other, we experimented in the field to see how Ogasawara Islands Honeyeaters responded to unfamiliar food in two different situations: with and without the presence of Japanese White-eyes. Japanese White-eyes are not evenly distributed across the island, and there are almost none in some areas inhabited by Ogasawara Islands Honeyeaters. Therefore, we could compare the behavior of Ogasawara Islands Honeyeaters in allopatric and sympatric areas. The population densities of Ogasawara Islands Honeyeaters in the allopatric and sympatric areas were about seven and four individuals per hectare, respectively. The population density of Japanese White-eyes in the sympatric area was 30–40 individuals per hectare.

In forests on Hahajima Island 25 feeding stands were set up. Eleven were set up in the allopatric area of Ogasawara Islands Honeyeaters, and the remaining 14 in the sympatric area shared by the two species.

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On the stands we used peaches in syrup as unfamiliar food, since we believed that the Ogasawara Islands Honeyeater had never eaten these before. The peaches were cut in half and about 8 cm in diameter. The feeding stands, made of plastic, were fixed to naturally growing trees with steel wire, about 1 m above ground level, close to thin branches suitable for birds to perch on (Fig. 1). We selected trees that had at least one side clear of heavy foliage so that the birds could find the feeding stands. The survey was carried out in November and December 1996.

During the experiment, the food was replaced daily. And each day the food was checked for evidence of pecking. When pecking marks were found, we observed the behavior of the birds that came to the stands. The responses of the two species were recorded from 8:00 am to 12:00 noon on the first and 15th days of the experiment. Responses were classified as one of three types: "no approach", "approach only", and "approach and ingest". "Approach" was defined as a situation where an individual came within 1 m of the feeding stand.

On the first day of the experiment, the response of Ogasawara Islands Honeyeaters was not significantly different in the allopatric and sympatric areas (Fig. 2, Fisher's exact probability test, $P=0.6232$). No Ogasawara Islands Honeyeaters ate the food in either area, but individuals did approach it. In the sympatric area, Japanese White-eyes ate the food from the first day on all the stands except one, where food was eaten from the second day onwards. Japanese White-eyes approached the stands every day and always ate the food. We often observed Ogasawara Islands Honeyeaters watching the Japanese White-eyes foraging. On the 15th day, Ogasawara Islands Honeyeaters ate a significant amount of the previously unfamiliar food in the sympatric area (Fig. 2, Fisher's exact probability test, $P=0.0001$). The test was between the sympatric and allopatric areas. In the allopatric area, the honeyeaters often approached the feeding stands but never ate the bait.

These results suggest that Ogasawara Islands Honeyeaters learned what food to eat from the behavior of Japanese White-eyes. It is known that the two species sometimes form mixed-species flocks during the non-breeding season (Ueda 1990), suggesting that at least one species should enjoy a benefit from the behavior. Some bird species are known to increase food acquisition by participating in mixed-species flocks (Vijayan 1989, Sasvari 1992, Valburg 1992). We have observed Japanese White-eyes foraging on

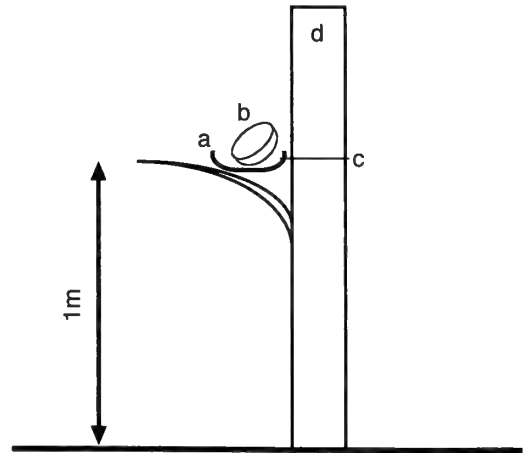


Fig. 1. A feeding stand on a tree trunk. a) plastic feeding stand, b) peaches in syrup, c) steel wire, d) naturally growing tree.

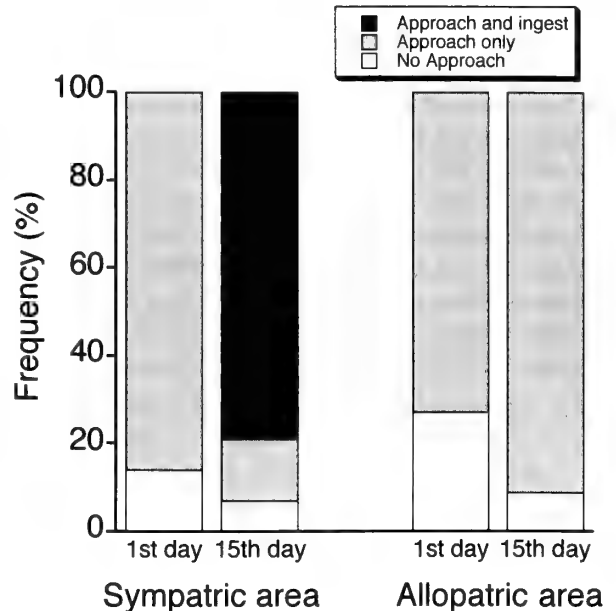


Fig. 2. Responses of Ogasawara Islands Honeyeaters to unfamiliar food in allopatric and sympatric areas on the first and 15th day of the experiment. The y-axis shows the frequency of feeding stands classified to each response type of all feeding stands in each of the two areas. The sample sizes for the sympatric and allopatric areas are 14 and 11, respectively.

introduced fruit, and Ogasawara Islands Honeyeaters watching their behavior in mixed-species flocks. There is a possibility that Ogasawara Islands Honeyeaters have started eating unfamiliar foods by learning from the behavior of Japanese White-eyes in such circumstances.

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TECHNICAL NOTE

Molecular sexing of individual Ryukyu Robins *Erithacus komadori* using buccal cells as a non-invasive source of DNAORNITHOLOGICAL
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Buccal cells have been used as a good and non-invasive source of DNA for humans (Feigelson et al. 2001), experimental animals (Zimmerman et al. 2000), livestock (Kwon et al. 1993), and wild primates (Hashimoto et al. 1996), but have not been used for wild birds. Blood is the most commonly used source of DNA for avian molecular ecological studies because safe and effective sampling techniques have been well-developed (reviewed in Wingfield 1999), hence other non-invasive methods have not been deemed necessary.

In the case of the Ryukyu Robin *Erithacus komadori*, endemic only to southwestern Japan (Kawaji & Higuchi 1989), however, blood sampling is difficult. Because of its limited distribution and the steep population declines on some islands, it has been designated as a “national natural treasure” and “national endangered species of wild fauna and flora” of Japan. Consequently, both the Kagoshima prefectural government and the national agency for cultural affairs are against taking blood samples from robins, especially from nestlings, for political and cultural reasons. However, in order to reveal sex-related mortality and dispersal distances of sexually monomorphic fledglings, molecular sexing is needed (Seki 2002). Here I report the results of molecular sexing of adult robins using DNA extracted from buccal cells, comparing them with those from blood, and examine the reliability of buccal cells as a source of DNA for avian sexing.

Samples of both buccal cells and blood were obtained from 20 male and 20 female adult Ryukyu Robins, that had been previously sexed based on morphological characteristics. Robins were captured (under license by mist-net) during the breeding season, from 15 April to 30 June 2002, on Nakanoshima

Island, Kagoshima, Japan.

Buccal cells were collected by rolling cotton swabs against the inside of each robins' mouth and throat five times. Each swab was put into a microtube and soaked in 1 ml of preservation buffer (150 mM NaCl, 10 mM Tris-HCl pH 8.0, 10 mM EDTA), and kept at room temperature during the one week it took to transport them to the laboratory, where they were stored at 5°C for up to one month (see also Appendix 1 for longer preservation). After adding 10 µl of 10%-SDS, the samples were digested with proteinase K (5 µl of 20mg/ml) at 55°C for one hour and an additional 16 hours at 37°C. DNA was then extracted by the conventional phenol/chloroform method. Up to 30 µl of blood samples were obtained by brachial vein puncture and no ill effects were recorded. Blood samples were stored in GenTLE solution I (Takara) at room temperature and DNA was extracted using an extraction kit (QIAamp DNA Blood Mini Kit, QIAGEN) within 10 days of sampling.

The sex of each individual was determined by length polymorphism at the chromo-helicase-DNA-binding (CHD) gene, using Ellegren & Fridolfsson's (1997) primer set 3007F (5'-TACATACAGGCTCTACTCCT-3') and 3112R (5'-CCCCCTTCAGGTCTTTTAAA-3'), following the methods used by Fridolfsson & Ellegren (1999). All PCR reactions were performed in 25 µl volumes on a Perkin Elmer 9600 Thermal Cycler, using *Taq* DNA polymerase (Takara *Taq*, Takara). Each reaction mixture contained 0.625 unit of *Taq*, 200 µM dNTPs, 20 mM Tris-HCl pH 8.0, 50 mM KCl, 2 mM MgCl₂, 5 pmol of primers. The thermal profile comprised an initial denaturing step of 94°C for two minutes, followed by a “touch-down” scheme where the annealing temperature was lowered by 1°C per cycle, starting from 60°C until a temperature of 50°C was reached. Then 35 additional cycles were run at a constant annealing temperature of 50°C. Denaturation was at 94°C for

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30 s, annealing for 30 s, and extension at 72°C for 40 s, and a final extension step of five minutes was added after the last cycle. PCR products were separated in 2.5% agarose gels (NuSieve GTG, BMA), run in standard TBE buffer and made visible using ethidium bromide staining.

PCR products from blood DNA gave clear bands for all 40 individuals, which could be sexed on the basis of distinct size differences between the CHD-W and CHD-Z gene copies, a single band for males and double bands for females (Fig. 1). Band patterns from buccal cells were the same as those from blood samples, and all the individuals were correctly sexed, using the DNA extracted by the conventional method. Thus buccal cells have been confirmed as a reliable source of DNA from wild birds. Buccal cell sampling is particularly suitable for the molecular sexing of nestlings as sampling takes less time than drawing blood, and because there is no need for disinfection and homeostasis. Safe sampling using this technique does not require extensive training, and only cotton swabs are required. It should be noted, however, that young, blind nestlings misidentify the cotton swabs as food being provided by the parents and so try to swallow them.

Blood sampling from young nestlings has been preferred in studies of avian sex allocation (e.g. Komdeur et al. 1997; Nishiumi 1998), presumably so as to have large enough sample sizes for analysis under conditions of high nest predation risk in the wild. In such situations, the buccal cell sampling would obviously reduce the stress for the nestlings

and their parents compared to blood drawing. The only negative aspect of buccal cell sampling is that DNA yields (1.3 ± 0.7 mg, Mean \pm SD, rough estimates using a spectrophotometer) are low compared to blood sampling, nevertheless it is sufficient for sexing, and also for other molecular studies using PCR.

Urine and feathers are other less- or non-invasive sources of DNA used in avian molecular ecological studies (Wingfield 1999). Urine samples, however, contain PCR inhibiting substances and food-origin compounds (Reed et al. 1997; Yamauchi et al. 2000; Nota & Takenaka 1999; Robertson et al. 1999), and for the Ryukyu Robin sexing success using urine samples was just 15% ($n=20$) (Seki 2003), thus buccal cells were preferred. Feather samples, especially plucked feathers, are also a reliable source of DNA (Segelbacher 2002), but care must be taken when removing growing feathers from nestlings (Wingfield 1999) and feathers are, of course, not available from naked nestlings.

Non-invasive sampling is becoming important for molecular studies of free-ranging animals (Segelbacher 2002), thus buccal cell sampling provides a preferable, easily performed, safe technique suitable for most studies of adults that requires only small amounts of DNA.

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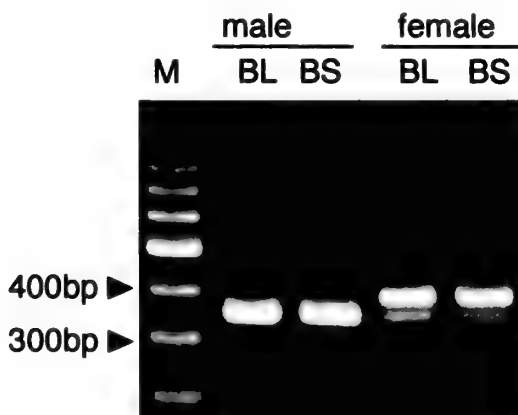


Fig. 1. Band patterns of male and female Ryukyu Robins, using the template DNA from two types of samples, blood (BL) and buccal swabs (BS). The lanes marked 'M' contain 100 bp DNA ladder. Primers 3007F and 3112R give one short fragment in males (CHD-Z) and two fragments in females (CHD-Z and CHD-W).

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APPENDIX 1

Buccal cells can also be kept in 99% ethanol when long-term preservation at room temperature is necessary, by rotating the sampling swab in the microtube filled with 1 ml of ethanol for about 10 seconds. Before the extraction, I centrifuged the microtube at 6,000×g (8000 rpm) for 10 minutes, discarded the ethanol without disturbing the pellet of cells, and allowed the pellet to dry. Although the DNA yield was lower by this method than when keeping cotton swabs in the buffer, it was still enough for sexing.

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Vol. 2 2003



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CONTENTS OF VOLUME 2

Number 1 February 2003

SPECIAL FEATURE

Ecology of seed dispersal

Ueda K

Introduction.

1

Kominami Y, Sato T, Takeshita K, Manabe T, Endo A & Noma N

Classification of bird-dispersed plants by fruiting phenology, fruit size, and growth form in a primary lucidophyllous forest: an analysis, with implications for the conservation of fruit-bird interactions.

3

Takanose Y & Kamitani T

Fruiting of fleshy-fruited plants and abundance of frugivorous birds: Phenological correspondence in a temperate forest in central Japan.

25

Hayashida M

Seed dispersal of Japanese stone pine by the Eurasian Nutcracker.

33

Fukui A

Relationship between seed retention time in bird's gut and fruit characteristics.

41

Rakotomanana H, Hino T, Kanzaki M & Morioka H

The role of the Velvet Asity *Philepitta castanea* in regeneration of understory shrubs in Madagascan rainforest.

49

ORIGINAL ARTICLES

Fujita M & Kawakami K

Head-bobbing patterns, while walking, of
Black-winged Stilts *Himantopus himantopus*
and various herons. 59

Tajima K & Nakamura M

Response to manipulation of partner
contribution: A handicapping experiment in
the Barn Swallow. 65

SHORT COMMUNICATION

Nagata H & Sodhi NS

Low prevalence of blood parasites in five
Sylviidae species in Japan. 73

A List of Referees 2002

75

Abstracts of the Japanese Journal of Ornithology, Volume 51

75

Number 2 September 2003

INVITED ARTICLES

Komdeur J

Adaptations and maladaptations to island
living in the Seychelles Warbler. 79

Pierre JP

Translocations in avian conservation:
reintroduction biology of the South Island
Saddleback (*Philesturnus carunculatus*
carunculatus). 89

Peh KS-H & Chong FL

Seed dispersal agents of two *Ficus* species in
a disturbed tropical forest. 119

SHORT COMMUNICATIONS

Yoshimura M, Hirata T, Nakajima A & Onoyama K

Ants found in scats and pellets taken from the
nests of the Japanese Wryneck *Jynx torquilla*
japonica. 127

ORIGINAL ARTICLES

Mizuta T, Yamada H, Lin R-S,

Yodogawa Y & Okanoya K

Sexing White-rumped Munias in Taiwan,
using morphology, DNA and distance calls. 97

Matsubara H

Comparative study of territoriality and habitat
use in syntopic Jungle Crow (*Corvus macro-*
rhyncos) and Carrion Crow (*C. corone*). 103

Hamao S

Reduction of cost of polygyny by nest
predation in the Black-browed Reed
Warbler. 113

Kawakami K & Higuchi H

Interspecific learning by the Ogasawara Islands
Honeyeater *Apaloeteron familiare* from the
Japanese White-eye *Zosterops japonicus* on
Hahajima, the Bonin Islands, southern
Japan. 132

TECHNICAL NOTE

Seki S-I

Molecular sexing of individual Ryukyu Robins
Erithacus komadori using buccal cells as a
non-invasive source of DNA. 135

Instructions to Authors

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General Instructions

1) Cover page

The title page should contain the title, author names, affiliations, addresses, contact name and address (phone and/or facsimile number together with an e-mail address) for correspondence. Authors with different affiliations should be identified with superscripts. On the same page, a running title (less than 40 letters) and the number of tables and figures are also required. To discriminate the family name(s) from the first and/or the middle owns, contributors are encouraged to spell their family names in all capitals.

2) Abstract and key words

Abstracts should be less than 300 words, followed five or less key words in alphabetical order.

3) Names of animals and plants

Scientific names of species should be given both in the abstract and in the article at the first mention. Scientific and English names of birds should follow an authoritative source. Capitals should be used for the initial letters for each word of English names (e.g., Black-billed Magpie) but not for a group name (e.g., crows).

4) References

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All measurements should be given in SI units. Time should be shown as 0930 and 1500 and the geographical location as 35°20′25″N, 136°10′20″E. Statistical symbols should be capitalized except df (e.g., SD, SE, P, N). Italicized expressions are not preferred.

6) Tables and Figures

The contributors are supposed to take the size of the printed page into consideration when they prepare their tables and figures: the actual print is on 165×223 mm in double columns with 80 mm width.



ORNITHOLOGICAL SCIENCE

Volume 2 Number 2 September 2003

Contents

INVITED ARTICLES

Komdeur J

- Adaptations and maladaptations to island living in the Seychelles Warbler. 79

Pierre JP

- Translocations in avian conservation: reintroduction biology of the South Island Saddleback (*Philesturnus carunculatus carunculatus*). 89

ORIGINAL ARTICLES

Mizuta T, Yamada H, Lin R-S,

- Yodogawa Y & Okanoya K
Sexing White-rumped Munias in Taiwan, using morphology, DNA and distance calls. 97

Matsubara H

- Comparative study of territoriality and habitat use in syntopic Jungle Crow (*Corvus macro-rhynchos*) and Carrion Crow (*C. corone*). 103

Hamao S

- Reduction of cost of polygyny by nest predation in the Black-browed Reed Warbler. 113

Peh KS-H & Chong FL

- Seed dispersal agents of two *Ficus* species in a disturbed tropical forest. 119

SHORT COMMUNICATIONS

Yoshimura M, Hirata T, Nakajima A & Onoyama K

- Ants found in scats and pellets taken from the nests of the Japanese Wryneck *Jynx torquilla japonica*. 127

Kawakami K & Higuchi H

- Interspecific learning by the Ogasawara Islands Honeyeater *Apalopteron familiare* from the Japanese White-eye *Zosterops japonicus* on Hahajima, the Bonin Islands, southern Japan. 132

TECHNICAL NOTE

Seki S-I

- Molecular sexing of individual Ryukyu Robins *Erithacus komadori* using buccal cells as a non-invasive source of DNA. 135

S 3804

ISSN 1347-0558

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HISTORY MUSEUM
29 APR 2004

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日本鳥学会 2004 年度大会のご案内

URL: <http://gi.ics.nara-wu.ac.jp/OSJ04/>

日本鳥学会 2004 年度大会を以下の要領で開催いたします。皆さまふるってご参加ください。

1. 会期 2004 年 9 月 17 日（金）～20 日（月祝日）

2. 会場 奈良女子大学（奈良市北魚屋西町）

交通案内は「15.」の会場アクセスをご覧ください。

3. 日程

7 月 16 日（金） 参加申し込み、諸費用事前振込及び要旨・主旨締め切り

	午前	午後	夜
9 月 17 日（金）		各種委員会及び評議委員会	自由集会
9 月 18 日（土）	口頭発表	ポスター発表	自由集会
9 月 19 日（日）	ポスター発表	総会 シンポジウム	懇親会
9 月 20 日（月祝日）	口頭発表	自由集会	

4. 参加申し込み

大会に参加される方は、綴じ込みの大会申し込み用紙を切り取るかコピー、もしくは大会ウェブサイト <http://gi.ics.nara-wu.ac.jp/OSJ04/> からダウンロード印刷して、「参加申し込み」欄に必要事項を記入の上、7 月 16 日（金）までに大会事務局にお送りください。郵送のみ受け付けます（当日消印有効）。

5. 一般講演

一般講演を希望される方は、大会申し込み用紙の「一般講演申し込み」欄に必要事項を記入し、「8.」の要領で作成した講演要旨を大会事務局宛に 7 月 16 日（金）までにお送りください。なお、一般講演の申し込みは演者のみが行ってください。

一般講演は口頭発表またはポスターとします。発表者は原則として日本鳥学会会員でなければなりません。共同発表の場合は、発表者の中に会員が含まれていることが必要です。一般講演は一人一題に限ります。同一発表者が複数の一般講演で演者となることはできません。

口頭発表は発表時間 12 分、質疑応答 2 分 30 秒を厳守していただきます。原則として OHP による発表に限らせていただきます。OHP はご自分で操作していただきますのでご協力をお願いします。

ポスターのサイズは現時点では未定です。決定次第、大会ウェブ上でご案内します。ポスター発表の時間帯は、18 日午後と 19 日午前の 2 つを設けていますが、演題が多い場合には 2 つのセ

セッションに分け、それぞれのセッションの開示前にポスターを展示し、終了後に片づけていただくことになります。ポスターサイズを含めた詳細については逐次大会ウェブ上でお知らせします。また、ポスタートーク（OHPを使った2分間の口頭による宣伝）の時間を設ける予定です。

6. 高校生のポスター発表

昨年度大会に続き、高校生の生物等のクラブによる鳥類に関する研究のポスター発表コーナーを設けます。発表者に会員資格は不要です。また、発表団体に属する高校生は参加費は不要です。希望団体は大会事務局にご連絡ください。

鳥学の研究を行っている高校のクラブをご存知の会員の方は、参加を勧めていただければ幸いです。発表は一般公演のポスター発表と同じで、ポスタートークもできます。「8.」の要領で要旨を作成し事務局に提出してください。

7. 自由集会

9月17日、18日の夜、及び20日の午後に2時間程度の自由集会の時間帯を設けます。開催を希望される責任者の方は、大会申し込み用紙の「自由集会開催申し込み」欄に必要事項を記入し、「8.」の要領で作成した自由集会開催主旨を7月16日（金）までに大会事務局宛にお送りください。会場数には限りがありますので、計画が決まり次第、事前に連絡を頂けると助かります。自由集会会場にはOHP及びPCプロジェクターを用意します。自由集会における会場の運営・後片づけは、主催者の責任で行ってください。

8. 講演要旨及び自由集会開催主旨

一般講演及び高校生のポスター発表を希望される方は、以下の例に倣って、講演内容を簡潔にまとめた講演要旨を作成してください。

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ここから本文。

自由集会の開催責任者の方は、集会の目的と内容を簡潔にまとめた自由集会開催主旨を講演要旨のスタイルに習って作成してください。

これらの要旨・主旨はコピーを一部とり、計2部を大会申し込み用紙と一緒に7月16日（金）

までに大会事務局にお送りください。

一般講演要旨・自由集会主旨は電子媒体での提出も受け付けます。テキスト形式で大会事務局までお送りください。図を貼り込む場合は、本文・図ともに1つのpdfファイルにまとめてお送りください。大会ウェブ上のプログラムにて公開いたします。電子媒体で提出される方も、紙に印刷コピーした要旨・主旨を忘れずに郵送願います。

9. シンポジウム

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場所：奈良女子大学講堂

5人（うち外国人3名）の演者による話題提供とコメンテータによる総括を含みます。近日中に詳細な内容を大会ウェブ上に掲示します。

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3) 講演要旨集のみ 一般・学生ともに 3000 円

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11. 締め切り

事前申し込み（参加申し込み、一般講演要旨・自由集会主旨の提出、諸費用振込）の締め切りは、7月16日（金）（消印有効）です。これ以降、参加費・懇親会費は割り増しとなります。また、懇親会は会場準備の都合で、事前申し込み締め切り以降の申し込みをお受けできない場合があります。あらかじめご了承ください。

12. 総会委任状

大会期間中に総会が開催され、学会の重要な議題が審議されます。総会に参加されない方は、大会申し込み用紙の末尾の総会委任状に記入捺印の上、大会事務局までお送りください。

13. 大会決議

総会において、保護に関する決議文案等の提出を希望される方は、なるべく早く、遅くとも総会

の1ヶ月前(8月19日)までに、日本鳥学会保護委員会・尾崎清明委員長にご連絡の上、同委員会とご相談ください。あらかじめ相談のない提案には対応しかねますのでご了承ください。

14. 懇親会

9月19日夜に、奈良女子大学学生会館の学生食堂で開催予定です。参加ご希望の方は、7月16日(金)までに懇親会費をお支払いください。

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奈良女子大学は近鉄奈良駅から徒歩5分。JR奈良駅から徒歩15分です。京都からは近鉄京都線で近鉄奈良駅まで約45分。新大阪からはJR大阪環状線鶴橋経由近鉄奈良線で近鉄奈良駅まで約50分です。詳しくは大会ウェブサイトをご覧ください。

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18. 大会事務局

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大会会長兼事務局長

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日本鳥学会2004年度大会参加申込用紙

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日本鳥学会2004年度大会事務局

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SPECIAL FEATURE

Invasive bird species

INTRODUCTION

For the past hundred and so years, we have been transforming the planet at a very rapid rate. We have heavily altered natural habitats and created new spaces and opportunities for invasive bird species, whether exotic or native. These species arrive in anthropogenically-altered areas, on their own or aided by humans. Many of these species establish self-sustaining populations in the newly colonized areas. Some are perceived as a nuisance because they threaten native species, others because they are thought to carry and spread disease to humans, yet others because they are considered unattractive in some way. Sometimes, managers and politicians come under public pressure to devise management strategies to curb or eradicate the populations of these new arrivals.

Humans are responsible not only for creating conducive environment for the invasive species but also for directly assisting their introduction themselves (e.g. by releasing caged birds). Birds feature prominently in invasion ecology as historical records of bird species introductions are available from various locations around the globe. Worldwide, 1400 attempts to introduce 400 exotic bird species have been recorded. Most bird introductions initially took place during the eighteenth and nineteenth centuries, coinciding with the periods of major European expansion and settlement. Birds were introduced by settlers predominantly for aesthetics, hunting and biological control. Two-thirds of the species chosen for introduction belonged to 6 of 145 bird families: Anatidae (ducks), Columbidae (pigeons and doves), Fringillidae (finches), Passeridae (sparrows), Phasianidae (pheasants) and Psittacidae (parrots). This over-representation of certain families highlights the reasons for their introductions. For example, ducks and pheasants were introduced for hunting whereas parrots, sparrows and finches were introduced as pets. Human rapid modification during the twentieth century has also realized a rapid spread of invasive birds.

The negative impact of invasive species on native biodiversity and ecosystems has been widely recognized. In addition, some invasive species can be devastating to the human economy. As mentioned, most introductions of exotic species to new areas are the direct or indirect results of human activities. Therefore social and economic factors are often as critical as biological factors in the introduction of exotic species. Human activities such as logging and grazing create optimal habitats for colonization by many exotic species. Agriculture also facilitates species invasions. Exotics in agro-ecosystems are exposed to agricultural practices for many generations, resulting in selection for characteristics that make them persistent and noxious.

Despite the concern over the negative impact of invasive species, invasive ecology remains a fledgling field with many questions unanswered. Basic ecological data on the invasive species remain poor, particularly in Asia. With this special feature, we hope to create a scientific awareness about the invasive species, and hence stimulate further research on them. We have used a very loose definition of invasive species. Regardless of their impact, we have considered all non-native or native bird species that have established either through natural range expansion or deliberate release into human-dominated landscapes. We have included all these species to show that not all invasive species are harmful. In fact, some invasive bird species can assist in ecological processes such as seed dispersal or pollination. We hope that this approach will provide a better understanding of the ecological impact and role of bird invaders.

There are six papers in this special feature. Eguchi and Amano's paper reports on the spread of various exotic species in Japan. They note that currently the Japanese public's concern about the exotic birds remains low. Nonetheless, they offer numerous management recommendations to control the spread of exotic birds in Japan. Kawakami and Yamaguchi report on the spread of the Melodious Laughing Thrush (*Garrulax canorus*) in Japan. They show that the spread of this species is possibly limited by elevation and snowfall. Tojo and Nakamura studied the exotic Red-billed Leiothrix (*Leiothrix lutea*) on Mt. Tsukuba. They suggest that there

be little impact of this species on native forest birds in the study area.

In his paper, Brook reviews exotic bird introductions to Australia, New Zealand and surrounding islands. He reports that of more than 242 bird species that were introduced to these areas, only 32% established viable populations. Brook also identified ecological traits (e.g. behavioural flexibility) that may have given certain species colonization success. Leven and Corlett review bird invasions into Hong Kong. They suggest that although some exotic bird species may have invaded Hong Kong close to or earlier than 1860, most species have done so after this time. They review the possible impact of these invaders but suggest that much remains unknown. Yap and Sodhi review bird invasions into Southeast Asia. They review the impacts of the invasive bird species on Southeast Asian economy and biodiversity. They explore the efficacy of different management options. Yap and Sodhi's review shows that there is a paucity of studies on the status and effects of invasive birds in Southeast Asia.

We hope that this special feature will be of interest not only to ornithologists but also to the scientists working in invasion ecology.

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Spread of exotic birds in Japan

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ORNITHOLOGICAL SCIENCE

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Abstract Introduction of exotic birds into Japan has been increasing. So far, forty-three species have bred at least once here. Most of these exotic species were imported as caged birds and entered the natural environments either accidentally or deliberately. Dominant taxa are Psittacidae, Passeridae (Estrildinae and Ploceinae) and Sturnidae. Most of the exotic birds are established in habitats disturbed by humans such as reed beds, riparian grasslands, croplands, and towns. Exceptions are Timaliidae such as the Red-billed Leiothrix *Leiothrix lutea* and the Melodious Laughing Thrush *Garrulax canorus*, which have invaded indigenous forests. Although most species are restricted to small particular areas, the Red-billed Leiothrix has been rapidly increasing and expanding its geographical range. Serious adverse influences by introduced birds on local ecosystems, biota and human economic resources have not been pronounced yet in Japan, except for crop damage or other economic damages by the Feral Pigeon *Columba livia* and Light-vented Bulbul *Pycnonotus sinensis formosae*. Therefore, public concern about avian introduction is low in Japan. Strict control of import of exotic birds, a registration system of caged birds, eradication and management of established exotic birds, and more research and public education about avian introduction are necessary.

Key words Introduced birds, Invasive birds, Naturalization

Many birds have been transported by humans to new areas of the world. In the late nineteenth and early twentieth centuries, many European immigrants introduced birds of Europe and eastern Asia for esthetic purposes into New Zealand, Australia, the Hawaiian Islands and North America (Long 1981; Lever 1987). These introductions were made deliberately and continually by organizations such as the Acclimatization Society, MayHua Club, or Honolulu Mejiro Club (Long 1981; Lever 1987; Simberloff & Boecklen 1991). They left records of release site, date and size of release (Simberloff & Boecklen 1991; Veltman et al. 1996). In many islands in the Pacific and Indian Oceans, birds were released for pest control (Long 1981; Lever 1987; Simberloff & Stiling 1996). Records of such intentional introductions are also available. Based on these records, many studies have been conducted on ecological factors determining the introduction success (cf. McLain et al. 1995; Veltman et al. 1996; Green 1997; Duncan et al.

1999; Sorci et al. 1998; Sol & Lefebvre 2000; Blackburn & Duncan 2001; Sol et al. 2002), and interactions among species (e.g. Moulton & Pimm 1983, 1986; Simberloff & Boecklen 1991; Simberloff 1992; Duncan 1997).

Many birds have been also introduced into Japan (Narusue 1981; Nakamura 1990, 1994; Eguchi & Amano 1999, 2000). Most introductions have been caused by the accidental escape of caged birds. Such accidental releases of exotic birds were sporadic and local, and, therefore, records of introduction were seldom kept. Further, introduction of birds into Japan became prominent only over the past one or two decades. Therefore, public concern about avian introductions is not high and information is scarce. These situations make it difficult to study avian introductions into Japan. However, the increase in international trade and transportation in recent years raise the risk of avian introductions. In this study, we conducted a nation-wide investigation about the distribution of introduced birds in Japan, the first one in this country. In this paper, we discuss the introduction of birds into Japan, and focus mainly on the nature of

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introduction and potential influence on native biota.

AVIAN INTRODUCTIONS INTO JAPAN

Table 1 shows a list of exotic birds known to breed in Japan based on information collected by inquiries through e-mails to members of mailing lists ("jeconet" and "banding") and the Ornithological Society of Japan, through journals of Wild Bird Society of Japan (WBSJ), Sapporo Branch of WBSJ, Kitakyushu Branch of WBSJ and Japanese Society for Preservation of Bird, and personal inquiries from 2000 to 2001. In total, 36 species or subspecies are known to breed. Based on the literature, five other species are known to breed, the Alexandrine Parakeet *Psittacula eupatria*, Orange-cheeked Waxbill *Estrilda melpoda*, Yellow-crowned Bishop *Euplectes afer*, White-rumped Munia *Lonchura striata* and Lesser Masked Weaver *Ploceus intermedius* (Iozawa 2000; Ornithological Society of Japan 2000). Light-vented Bulbul *Pycnonotus sinensis formosae* invaded Okinawa Island, but it is unknown whether it was by natural expansion of its geographical range or introduction by humans (Kinjo 1998). In several of the Ryukyu Islands, the Common Peafowl *Pavo cristatus* escaping from zoos have naturalized and increased in population size (Tanaka & Takehara 2003; M. Izawa pers. comm.). Thus, forty-three exotic species have bred at least once.

Records of introductions are available only for a few species. The Black-billed Magpie *Pica pica sericea* was introduced from Korea to northern Kyushu in the late sixteenth century (Eguchi & Kubo 1992). The range of its population was restricted to small region for about 400 years after the establishment. However, the population size and geographical range have been increasing over the two or three decades while large-scale habitat changes were being made by humans (Eguchi & Takeishi 1997). According to historical documents, Feral Pigeons *Columba livia* had been seen around temples, shrines and towns from the seventeenth century. However, the first introduction of this species may date back more than six centuries further (Yamashina Institute for Ornithology 1979). For the Chinese Bamboo Partridge *Bambusicola thoracica*, two pairs were released in the vicinity of Tokyo for the first time in 1915 and thereafter introduction was repeated in various places so frequently that they have spread throughout Japan (Kuroda & Komiya 1987). The Ring-necked Pheasant *Phasianus colchicus karpowi* was introduced into

three main islands, Honshu, Shikoku and Kyushu, around 1920, but did not become established (Kuroda & Komiya 1987). On the other hand, introduction was started around 1930 and successful in Hokkaido where no closely related species were found. The Reeves' Pheasants *Symaticus reevesii* was released in Tochigi Prefecture and Tokyo in 1959 and 1960 and the Chukar Partridge *Alectoris chukar* in Izu Islands in 1960 for hunting (Kiyosu 1978). Escaped caged birds were seen from the early 1900s. For example, Kuroda (1913) reported a naturalized flock of Java Sparrows *Padda orizivora* and Chestnut Mannikins *Lonchura atricapilla* in the vicinity of Tokyo in 1910s. However, the little information available reports that most other exotic species were introduced only in past one or two decades.

So far, there have been no investigations done at a nation-wide scale. Narusue (1981) conducted a research about introduced birds around Tokyo and reported that breeding was confirmed for 19 species and one subspecies by 1980; i.e., the Budgerigar *Melopsittacus undulatus*, Alexandrine Parakeet, Indian Ring-necked Parakeet *Psittacula krameri manillensis*, Indian Moustached Parakeet *P. alexandri fasciata*, Red-crested Cardinal *Paroaria coronata*, Black-rumped Waxbill *Estrilda troglodytes*, Orange-cheeked Waxbill *E. melpoda*, Red Avadavat *Amandava amandava*, Nutmeg Mannikin *Lonchura punctulata topela*, Spice Finch *L. p. punctulata*, Java Sparrow, White-headed Mannikin *L. maja*, Chestnut Mannikin, Tri-colored Mannikin *L. malacca*, Paradise Whydah *Vidua paradisaea*, Lesser Masked Weaver, Common Myna *Acridotheres tristis*, Crested Myna *A. cristatellus*, Bank Myna *A. ginginianus*, and Asian Pied Starling *Sturnus contra*. Based on the various information, Nakamura (1990) listed 24 species as breeding exotic species found in Japan by 1990. In this study, we recognize more than 40 species breeding in Japan. Thus, although the information in the past is limited, it is possible that the number of breeding exotic species has increased nearly twice over a decade.

The Chinese Bamboo Partridge and Ring-necked Pheasant were introduced as game birds and the Feral Pigeon for food. Most other species originated from escapees (Table 1). Thus, introduced birds in Japan were the result of non-intentional release, which is different from cases in other countries; for example, intentional large-scale release in Hawaii and New Zealand (Moulton & Pimm 1983; Veltman et al. 1996; Green 1997).

Because most introductions were originated from escapees, dominant taxa are Psittacidae, Passeridae (Estrildinae and Ploceinae) and Sturnidae (Table 1). Species that have a long history of repeated introduction such as the Feral Pigeons and Chinese Bamboo

Partridge have expanded all over the country. However, because most other species have been introduced recently and release has been sporadic, they are seen only in small areas and in small numbers. The Red-billed Leiothrix *Leiothrix lutea* is an excep-

Table 1. Exotic birds breeding in Japan¹.

Order	Family	Species/Subspecies	Aim of introduction	Habitats in Japan ²
Anseriformes	Anatidae	<i>Cygnus olor</i>	esthetic	waters
		<i>Aix sponsa</i>	esthetic	waters
		<i>Cairina moschata</i>	foods	waters
Ciconiiformes	Ciconiidae	<i>Mycteria leucocephala</i>	esthetic	waters
Galliformes	Phasianidae	<i>Bambusicola thoracica</i>	hunting	forest
		<i>Phasianus colchicus karpowi</i>	hunting	forest, cropland
		<i>Colinus virginianus</i>	esthetic	forest, riparian
Columbiformes	Columbidae	<i>Columba livia</i>	foods	human habitations
Psittaciformes	Psittacidae	<i>Melopsittacus undulatus</i>	esthetic	human habitations, riparian
		<i>Myiopsitta monachus</i>	esthetic	human habitations
		<i>Psittacula krameri manillensis</i>	esthetic	human habitations
		<i>Psittacula alexandri</i>	esthetic	human habitations
Passeriformes	Pycnonotidae	<i>Pycnonotus jocosus</i>	esthetic	human habitations
	Timaliidae	<i>Garrulax perspicillatus</i>	esthetic	forest
		<i>Garrulax sannio</i>	esthetic	forest
		<i>Garrulax canorus</i>	esthetic	forest
		<i>Leiothrix lutea</i>	esthetic	forest
	Emberizidae	<i>Paroaria coronata</i>	esthetic	riparian, cropland
	Passeridae	<i>Estrilda troglodytes</i>	esthetic	riparian, cropland, human habitations
	(Estrildinae)	<i>Lonchura punctulata</i>	esthetic	riparian
		<i>Lonchura malacca</i>	esthetic	riparian
		<i>Lonchura atricapilla</i>	esthetic	riparian, cropland
		<i>Lonchura maja</i>	esthetic	riparian
		<i>Padda oryzivora</i>	esthetic	riparian, cropland
		<i>Amandava amandava</i>	esthetic	riparian
	Passeridae	<i>Vidua macroura</i>	esthetic	riparian
	(Ploceinae)	<i>Vidua paradisaea</i>	esthetic	riparian
		<i>Euplectes orix</i>	esthetic	riparian, cropland
		<i>Ploceus manyar</i>	esthetic	riparian
	Sturnidae	<i>Sturnus contra</i>	esthetic	human habitations
		<i>Acridotheres tristis</i>	esthetic	human habitations
		<i>Acridotheres ginginianus</i>	esthetic	human habitations
		<i>Acridotheres fuscus</i>	esthetic	human habitations
		<i>Acridotheres cristatellus</i>	esthetic	human habitations, riparian
	Corvidae	<i>Pica pica</i>	esthetic	human habitations, cropland
		<i>Urocissa caerulea</i>	esthetic	human habitations

¹ Based on information collected by inquiries through e-mails to members of mailing lists ("jeconet" and "banding") and the Ornithological Society of Japan, inquiries on journals of Wild Bird Society of Japan (WBSJ), Sapporo Branch of WBSJ, Kitakyushu Branch of WBSJ and Japanese Society for Preservation of Bird, and personal inquiries from 2000 to 2001. Species in which breeding is suspected by evidences such as breeding behavior, existence of juveniles, or grouping with adult males and females during the putative breeding season. Only species in which sightings at more than one place were obtained are included. Species in which the process of arrival into Japan is unknown is omitted.

² waters=river, lake, pond and estuary; forest=indigenous forests, woodlot and bamboo thicket; riparian=reed bed, riparian grassland and grassland; cropland=paddy field, cropland, and orchard; human habitations=park, town area, and human human habitations.

and has established populations successfully and expanded its range throughout mainly a southern half of the country.

Most exotic species are established in disturbed habitats near humans such as reed beds, riparian grasslands, croplands, and towns (Table 1), as are cases seen in other countries (Diamond & Veitch 1981; Moulton & Pimm 1983; Green 1984; Case 1996). Such a tendency in habitat selection may be a result of the competition with native species (Case 1996). However, it appears that it is also a reflection of the environments of their original habitats. For example, the original habitats of major introduced species from taxa such as Passeridae (Estrildinae and Ploceinae) and Sturnidae are savanna, cropland or dry woodland. Such habitats are similar to riparian grassland, cropland and parks in human habitations in Japan. Exceptions are species of the Timaliidae family, such as the Red-billed Leiothrix and the Melodious Laughing Thrush, which have invaded indigenous forests (Eguchi & Amano 2000; Sato 2000; Amano & Eguchi 2002a, b).

EFFECTS OF INTRODUCTION

Increasing population size of exotic species can exert a negative influence on the local ecosystem and native biota. In general, biotic invasion causes, 1) crop damage or other economic damage, 2) disturbance or destruction of habitats and ecosystem, and 3) decline or extinction of native biota (Long 1981; Lever 1987).

1) Crop damage and other economic damage

In America, 56% of 75 introduced species caused damages on agriculture and other economic resources (Temple 1992). Because many introduced birds inhabit disturbed habitats (e.g., cropland, human habitations), it is likely that the increase of such species may have an influence on agriculture and other human activity.

In Japan, several introduced species cause the crop damage or other economic damage. The Feral Pigeon is one of important pest birds damaging soybeans or other vegetables, and flocks roosting in storehouses, buildings or apartment houses cause the pollution with droppings (Yamashina Institute for Ornithology 1979). The Light-vented Bulbul invaded the Okinawa Island in mid 1970s and badly damaged fruits and vegetables (Kinjo et al. 1987; Kinjo 1998). The Black-billed Magpie builds a nest on an electricity

pole and this practice has been spreading among individual birds in recent years (Eguchi 1996), causing an increase in electrical accidents. The Ring-necked Parakeets are important pest bird of cereals and fruits both in its original habitats and introduced areas in North America and Europe (Feare 1996). This species has been increasing around Tokyo and adverse effects on agriculture in the suburbs are possible.

2) Influence on ecosystem and habitat

No cases of habitat destruction by introduced birds have been reported in Japan. However, if large birds are introduced and increase in numbers, adverse effects on the environment may be possible.

3) Influence on native avifauna

Predation

The Common Myna, Red-wiskered Bulbul *Pycnonotus jocosus* and Red-vented Bulbul *P. cafer* can be aggressive towards native bird species; e.g., egg breaking in Mascarenes and Tahiti (Jones 1996; Thibault et al. 2002; Blanvillain et al. 2003). If brood parasite species are introduced, new host species incapable of egg rejection would suffer serious losses in reproduction, e.g., the Brown-headed Cowbird *Molothrus ater* (Rothstein et al. 1980). So far, no cases have been reported of predation or brood parasitism by introduced species in Japan. However, *Vidua* species are a brood parasite in its original habitats. In Japan, two species of *Vidua* are known to breed (Table 1). Although host species have not been known yet, these species may influence on the breeding of native species. The Black-billed Magpie is a notorious predator of songbirds' nests in Britain (Gooch et al. 1991), but no such predation has been reported in Japan.

Disease

In the Hawaiian Islands, avian malaria has accompanied the invasion of introduced birds and reduced the number of native species (van Riper et al. 1986; Dobson & May 1991). In the Mascarenes Islands, avian pox and parrot diseases derived from introduced birds have prevailed (Jones 1996). Species on small and remote islands are particularly susceptible to new pathogen and parasites brought by introduced birds.

In Japan, prevalence of blood parasites is low in grassland living warblers and buntings (Sodhi et al. 1996, 1999; Nagata & Sodhi 2003). The mechanism

maintaining low parasite prevalence in grassland bird communities is unknown and it is possible that these parasite-free communities are vulnerable to invasion of new parasites. Introduced birds could act as a large reservoir of various parasites and pass them to native parasite-free birds.

Hybridization and Introgression

Introduced species can hybridize with native closely related species. This may cause the extinction of endangered native species. Sterility in hybrids results in wasted copulation, which causes a population decline. If it is fertile, introgressive hybridization results in a loss of original morphological traits in either species (Rhymer & Simberloff 1996; Allendorf et al. 2003). If introduced species outnumbers a native species, original traits of native species would disappear.

In Anatidae, interspecific hybridization occurs often and, in many cases, hybrids are fertile (Parkin 1996). In particular, introduced Mallards or domestic races have hybridized with native subspecies or native species, causing a decline in native species (Hunter 1996). The Hawaiian Duck *Anas wyvilliana* in Hawaii (Browne et al. 1993) and Grey Duck *A. superciliosa* in New Zealand (Gillespie 1985; Rhymer et al. 1994) have been decreasing due to introgressive hybridization with introduced Mallards *A. platyrhynchos*. In Japan, hybridization between domestic races of the Mallard and the Spot-billed Duck *A. poecilorhyncha* has been reported (Nakamura 1994), but effects on the latter's populations are not so severe yet.

In a polytypic species, introduction beyond a range of a particular subspecies causes a loss of original traits of each subspecies. In Japan, the Green Pheasant *Phasianus colchicus*, which comprises four subspecies lost originality in each subspecies due to introduction for hunting (Ornithological Society of Japan 2000). Reintroduction of endangered species should be carefully planned to reduce the likelihood of hybridizations.

Interspecific competition

The introduced Ruddy Duck *Oxyura jamaicensis* threatens the native White-headed Duck *O. leucocephala* with extinction through hybridization and interspecific competition in Britain (Hughes 1996). Hole-nesting introduced birds such as the European Starling *Sturnus vulgaris*, Common Myna and Ring-necked Parakeet can compete with native species for

nesting holes (Long 1981; Lever 1987; Feare 1996). In the Mascarenes Islands, there are some cases of interspecific competition, which caused a decline of native species, e.g., the Common Myna and Red-wiskered Bulbul affecting on the Mauritius Bulbul *Hypsipetes olivaceus* and Mauritius Cuckoo-shrike *Coracina typica*, the Madagascar Fody *Foudia madagascariensis* on the Mauritius Fody *F. rubra*, and the Ring-necked Parakeet on Mauritius Parakeet *Psittacula eques* (Jones 1996). In Hawaiian native forest, the Japanese White-eye *Zosterops japonica*, Melodious Laughing Thrush and Red-billed Leiothrix caused a decline of native species probably due to competition for food (Mountainspring & Scott 1985).

In general, however, it is difficult to demonstrate the existence of competition. Some authors think that extinctions of native species due to the competition with introduced species have been few (Diamond & Veitch 1981; Case 1991, 1996). Introduced species tend to inhabit environments disturbed by humans (Table 1), whereas native species inhabit undisturbed environments such as indigenous forests. Such a separation of habitat may be due to a difference in habitat selection, not interaction between these species (Diamond & Veitch 1981). Because of adapting to local habitats, native species would have a competitive advantage over introduced species. Therefore, introduced species seldom establish in indigenous forests due to competition from native species. Case (1996) attributes the success of introduced birds on islands to environmental changes by humans. However, between particular species, introduced species can outnumber native species even in indigenous forests due to demographic or environmental stochasticity or environmental heterogeneity (Sax & Brown 2000).

In the Hawaiian Islands, generalist species such as the Japanese White-eye and Timaliidae outnumbered native species specializing in a particular food resource (Mountainspring & Scott 1985). In oceanic islands, both habitat size and abundance of individual food resources are small. Usually, successful invasive species are a generalist (Jones 1996). Even in oceanic islands, introduced generalist species can become established and maintain a population by virtue of its wide niche. Such a introduced generalist may constantly interact with native species specializing in a particular resource and, because of its small niche width and a limited available resource, a native specialist may eventually decline its population size through interspecific competition.

The Red-billed Leiothrix has also invaded the deciduous broadleaved forests in Japan. This species dominates over the avifauna of such habitats in Kyushu (Eguchi & Masuda 1994; Eguchi & Amano 2000). In the avifauna of deciduous broadleaved forests, major species occupying a similar niche to this species are the Japanese Bush-warbler *Cettia di- phone*, Great Tit *Parus major*, Varied Tit *P. varius*, Coal Tit *P. ater*, Willow Tit *P. montanus* and Long-tailed Tit *Aegithalos caudatus*. Although there is no evidence to confirm the presence of interspecific competition between introduced and native species for food resources or nest sites, predation on Japanese Bush-warbler nesting in the same nesting habitat as the Red-billed Leiothrix has been found to be higher than in other regions where the latter species has not yet invaded (Amano & Eguchi 2002a, b). Even if there is no direct competition, a high density of Red-billed Leiothrixes may cause the decline of the reproductive success in sympatric species through apparent competition (Martin & Martin 2001) mediated by predator attraction.

PROBLEMS CAUSED BY INTRODUCED BIRDS IN JAPAN

Problems caused by avian introductions are different from those in other organisms in some areas. First, the introduction of birds does not cause as much public concern as in the cases of other organisms. As mentioned, the effects of introduced birds on the ecosystem, biota and human society are not obvious. Most introduced birds inhabit disturbed habitats. Therefore, introduced birds replace native species that have disappeared due to human disturbance and hence play a role in maintaining ecosystems and mitigating environments for human being (Case 1996). For example, introduced game birds occupy a similar niche held by now-extinct or rare native species and facilitate seed dispersal and germination of native plants in disturbed habitats in Hawaii (Cole et al. 1995). Therefore, people believe that because introduced birds are harmless compared to other animals such as mongooses in the Ryukyu Islands and feral goats in the Bonin Islands, they should be allowed to exist in disturbed habitats until they start to exhibit negative impacts on the ecosystem and humans.

Second, it is difficult to clarify the process and scale of introduction of birds in Japan. In recent years, there have been few large-scale introductions

like the ones done in New Zealand and Hawaii from the late nineteenth and early twentieth centuries. Instead, accidental and small-scale deliberate releases of caged birds are major sources of introductions into Japan. This makes it difficult to clarify the frequency and scale of introduction. Establishment and population growth of these escapees progress without attracting much attention, and such populations suddenly show up in large numbers that make regulation and eradication practically impossible. Many birds have been imported to Japan (Nash 1993; Melville 1994); more than two million every year by some estimates (Agency of the Environment 1986). Most of them are non-native species. Because many exotic birds have been imported into Japan, many escapees would establish self-maintaining populations.

Finally, it is nearly impossible to eradicate established exotic birds, both technically and psychologically. Generally, people cannot understand why a population already established in a habitat should be eradicated. For example, the Black-billed Magpie is an introduced species in Japan. Its population in northern Kyushu has increased in size over the past 20 to 30 years (Eguchi & Takeishi 1997). However, few people believe that this species should be eradicated just because it is an introduced species. The same situation is seen in the case of the Red-billed Leiothrix increasing in deciduous broadleaved forests throughout Japan.

Exotic species can establish populations in an undisturbed habitat and exert a negative effect on native species (Sax & Brown 2000). For example, timaliid birds like the Red-billed Leiothrix or Melodious Laughing Thrush have invaded into native forests in Japan and Hawaii, where they interact directly or indirectly with native species (Mountainspring & Scott 1985; Eguchi & Amano 2000; Amano & Eguchi 2002a, b). Increasing introductions of exotic birds increase the likelihood of escapees establishing populations in undisturbed habitats. This may increase the impact of such species on native species. So far, native species have declined in islands, such as the Hawaiian Islands, Tahiti, and Mascarenes Islands. In Japan, it is likely that the impact by introduced species will be serious in small islands such as the Ryukyu Islands.

LEGAL CONTROL OF AVIAN INTRODUCTION IN JAPAN

One basic measure against biotic introduction is

the legal control of introductions. The Ministry of the Environment has made a new Biodiversity Strategy in 2002 (<http://www/biodic.go.jp/nbsap.html>). It includes three main actions for biotic introduction, prevention, assessment and management (regulation and eradication). However, current legislation cannot control introduction effectively. Because most of the introduced birds and mammals in Japan are escaped captive animals, a legal barrier against the import of animals is necessary.

Basically the import of exotic species should be strictly regulated. The permission of import should be issued based on the risk assessment involving the abundance of the species in original countries, probability of establishment after escaping into non-original habitats, estimation of influences on native biota and difficulty of eradication of naturalized population. After issuing the permit, each individual should be registered and identified with a metal ring. An owner of the bird keeps the registration number and form. When a bird escapes or dies, the owner should notify its registration number and the escape or death to the permit issuing organization. Campaigns for preventing introductions of exotic species, including the threat of biotic invasion on the biodiversity, should be conducted for agents of import and bird fanciers.

Exotic species already naturalized should be eradicated as soon as they are recognized. Eradication in an early stage of introduction is essential. Eradication and regulation project of introduced birds should be conducted with a well-laid plan that has a feedback system that allows the project to be adjusted according to the result of each trial. Nation-wide monitoring of establishment of introduced birds is necessary to make plans for eradication and regulation. So far, investigations of introduced birds have been scarce and regional. Campaigns based on accurate and adequate information make it easy to obtain public approval for executing eradication and measurement project.

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The spread of the introduced Melodious Laughing Thrush *Garrulax canorus* in Japan

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Abstract The Melodious Laughing Thrush *Garrulax canorus* is an introduced species in Japan, and it has been recorded in the wild since the 1980s. The distribution of this species was estimated based on questionnaires. Four populations of this species have been confirmed in the western Kanto, northern Kyushu, southern Tohoku and Nagano Prefecture. There is a possibility that the expansion of this species is limited by elevational conditions and snowfall. Nevertheless, the distribution is still expanding. Therefore, it is necessary, as soon as possible, to assess the effect of the Melodious Laughing Thrush on the native birds.

Key words Conservation, Expansion of distribution, *Garrulax canorus*, Introduced birds, Melodious Laughing Thrush

The Melodious Laughing Thrush *Garrulax canorus* is an introduced species in Japan, and it has been observed in the wild since the 1980s (Sato 2000). The reason why this species naturalized in Japan is not clear. It is naturally distributed in southern China, Taiwan, Laos and Vietnam (Long 1981; Zheng 1982). It is a popular cage bird in China and Southeast Asia and a large number of individuals have been exported from Hong Kong (Nash 1999). This species has been imported into Japan since the seventeenth century (Isono & Uchida 1992). This species was introduced to the Hawaiian Islands in the early 1900s and to California in 1941 accidentally and purposely (Long 1981). While it failed to establish a population in California, it succeeded in naturalizing in the Hawaiian Islands, where it became the most common species below 1200 meters in elevation (Long 1981; Mountainspring & Scott 1985). The cause of disappearance in California is not known.

The Melodious Laughing Thrush prefers dense understory as breeding and foraging habitat and is sedentary in China and the Hawaiian Islands (Long 1981; Mountainspring & Scott 1985; Cheng et al. 1987). It is omnivorous and forages mainly on the ground for arthropods, earthworms, fruits and other

food (Long 1981; Cheng et al. 1987; Yamaguchi 2000; Kawakami 2002). This species was shown to have out competed native species on the Hawaiian Islands (Mountainspring & Scott 1985). Thus, there is concern that this species might give an impact the native species such as thrushes and bush-warblers that utilize the same prey and microhabitats (Kawakami 2002).

Thus far, the Melodious Laughing Thrush has been observed in northern Kyushu, in the Kanto, and in Fukushima Prefecture in Japan (Sato 2000; Yamaguchi 2000; Kawakami 2002). While it appears to be expanding its range in Japan (Sato 2000; Kawakami 2002), there is no study on its nationwide distribution to provide essential information for a management strategy. The aim of the present study is to show the past and present distribution of the species and to discuss factors limiting its population. With questionnaire, the distributions were clarified. With the data of recent distributions, we discussed on two limiting factors of range expansion: elevation and deepest snow depth of normal years. As the Melodious Laughing Thrush has been observed in lowland montane areas (Sato 2000; Yamaguchi 2000), there is a possibility that elevation limits its distribution. Since it frequently forages on the ground and is resident, deep snow might prevent it from foraging. We therefore compared its distribution with maps showing the

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the deepest snow depth of normal years.

METHODS

1) Questionnaires

Questionnaires were used to collect information on its distribution. As the Melodious Laughing Thrush spends much of its time in bushes, it is not easy to observe. However, its song is loud and conspicuous (Kawakami & Yamaguchi unpublished). Therefore, it is easy to detect its presence. Questionnaires were distributed through some mailing lists (Jeconet ML, Wildlife ML, Jbnest ML), newspapers (Sankei Shimbun 18 January 2000, Tokyo Simbun 27 January 2000, Asahi Shimbun 2 February 2000) and magazines ("Yacho" of Wild Bird Society of Japan, "Watashitachi no Shizen" of Japanese Society for Preservation of Birds, "Yacho Fukuoka" of WBSJ Fukuoka branch, "Kusunoki" of The Nature Interpreter Society of Fukuoka).

The questions were simple: 1) Have you seen or heard the Melodious Laughing Thrush? 2) If yes, when and where did you see or hear it? The morphological character was described with the questions as follows. "The body size is similar to the Dusky Thrush *Turdus naumanni*. Body color is bright brown, and there are white teardrop patterns around the eyes. The color of bills and legs is yellow". Questionnaires in newspapers and magazines also included photographs of the bird.

The Grey Starling *Sturnus cineraceus* is a very common bird species in Japanese lowlands, and it has similar morphological characters to the Melodious Laughing Thrush (i.e. similar body size, brown bodies, white pattern on their cheeks and yellow bills and legs). The two species can be easily confused with one another and some responses were misidentification. However, their ecological habits are very different. Especially, the Grey Starling prefers open habitats, while the Melodious Laughing Thrush prefers forests or bushes. Therefore, we excluded questionable answers from the analysis that involved ecological habits of Grey Starlings, such as "perching on wires side by side", "nesting under a roof" and "foraging at open habitats in residential areas". Responses were collected from January 2000 to August 2001.

2) Literature citation

Though the questionnaire method is useful to cover a wide area, its credibility is not high (Fujimaki &

Konishi 1996). In order to compensate for questionable information, we referred to the past reports of observations, specifically the Kanagawa chapter of WBSJ (1998), Kunihiro (1999), Sonoda (1999), Sato (2000), Yamaguchi (2000) and the records of inquiries on Melodious Laughing Thrushes at the Yamashina Institute for Ornithology.

3) Field detection

Based on the information of the questionnaire method, we investigated the existence of Melodious Laughing Thrushes at the edges of their distributions in western Kanto and southern Tohoku and Nagano Prefecture. The playback method was used to identify the species. This species readily responded to songs played on a tape recorder both in the breeding and non-breeding seasons (Kawakami & Yamaguchi unpublished). We played the songs in forests that had grown bushes near the edge of the distributions and recorded the existence of the species. This survey was conducted from January 2000 to August 2001.

4) The distribution and expansion of each population

We made distribution maps with grid maps consisting by square grids for each year based on the above information. Each grid was about 25 km² that was consisted of 5×5 grids based on standard grid data (Ministry of Environment 1997a-1). We calculated areas of 100% minimum convex polygon connecting the midpoint of each grid for each population for each year. Based on these values, we got the regression formula between the year and the square root of the area.

5) Snow depth and elevational conditions

In order to assess the influence of snowfall, the distribution map of the species was superimposed on the map showing the deepest snow depth of normal years (Japan Meteorological Agency 1993). And, in order to clarify the elevational conditions of the habitats, the elevation of each plot in which the species was recorded was classified into 6 categories, 0–200 m, 200–400 m, 400–600 m, 600–800 m, 800–1000 m and more than 1000 m. As there were plots that can not be recognized their reliable elevation, we excluded such data from analysis. The frequency of elevation data belonging to each category was shown for each population.

RESULTS

1) The distribution and expansion of each population

Four populations were identified at northern Kyushu, western Kanto, southern Tohoku and Nagano Prefecture (Fig. 1). We obtained 173, 557, 37 and 39 records by questionnaire for the four populations, respectively, and 184, 32 and 5 records by field detection for latter three populations, respectively. Figs. 2–5 show the distribution and expansion of each population. The Kyushu population originated in Fukuoka Prefecture in 1985 and expanded to southward. Melodious Laughing Thrushes were found in Fukuoka, Oita, Saga and Kumamoto prefectures in 2000. No map could be drawn for 2001 because no additional information was obtained for that year.

The first record of the Kanto population was reported at Fujino Town, Kanagawa Prefecture in 1987. The distribution extended in all directions along mon-

tane habitats. The eastward expansion stopped at the urban area. The species occurred in Kanagawa, Tokyo, Yamanashi, Saitama, Gunma and Shizuoka prefectures in 2001. The Tohoku population origi-

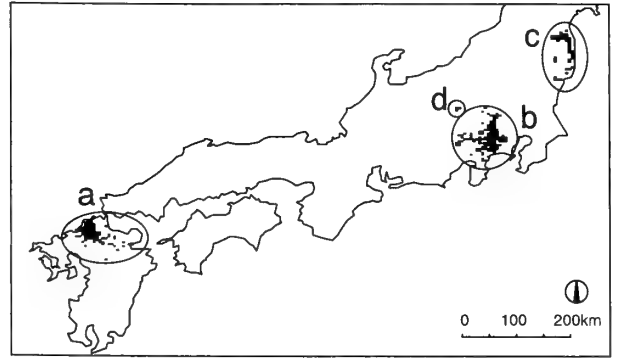


Fig. 1. The distribution of introduced Melodious Laughing Thrushes in Japan. a) The Kyushu population, b) The Kanto population, c) The Tohoku population, d) The Nagano population.

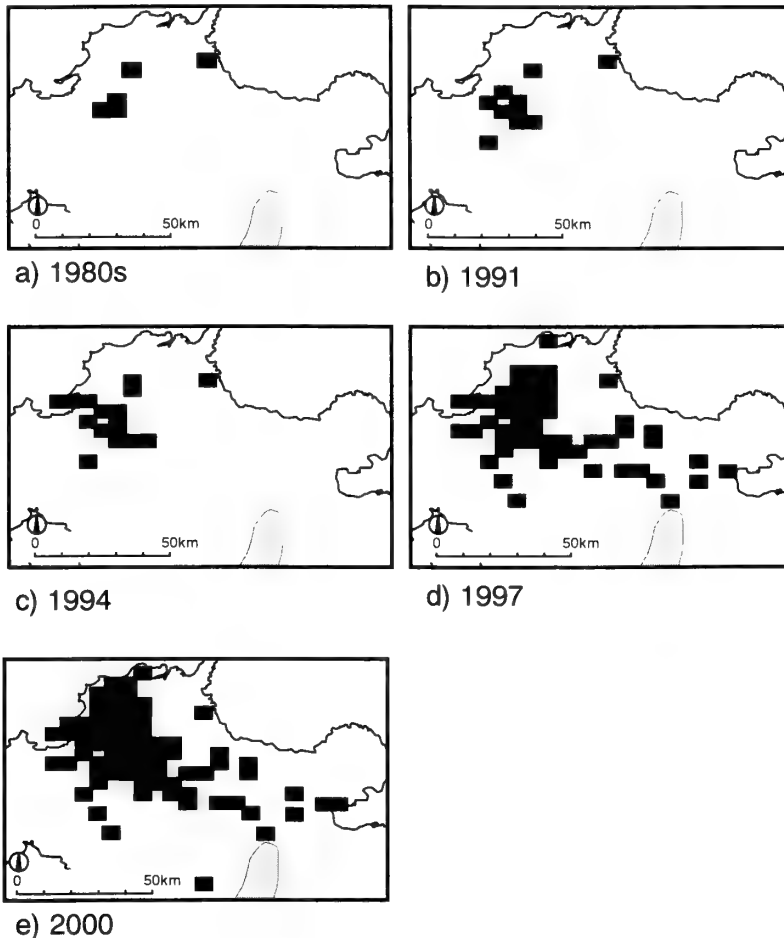


Fig. 2. The distribution of introduced Melodious Laughing Thrushes by year in Northern Kyushu. The gray area shows the range where the deepest snow depth of normal years is more than 20 cm.

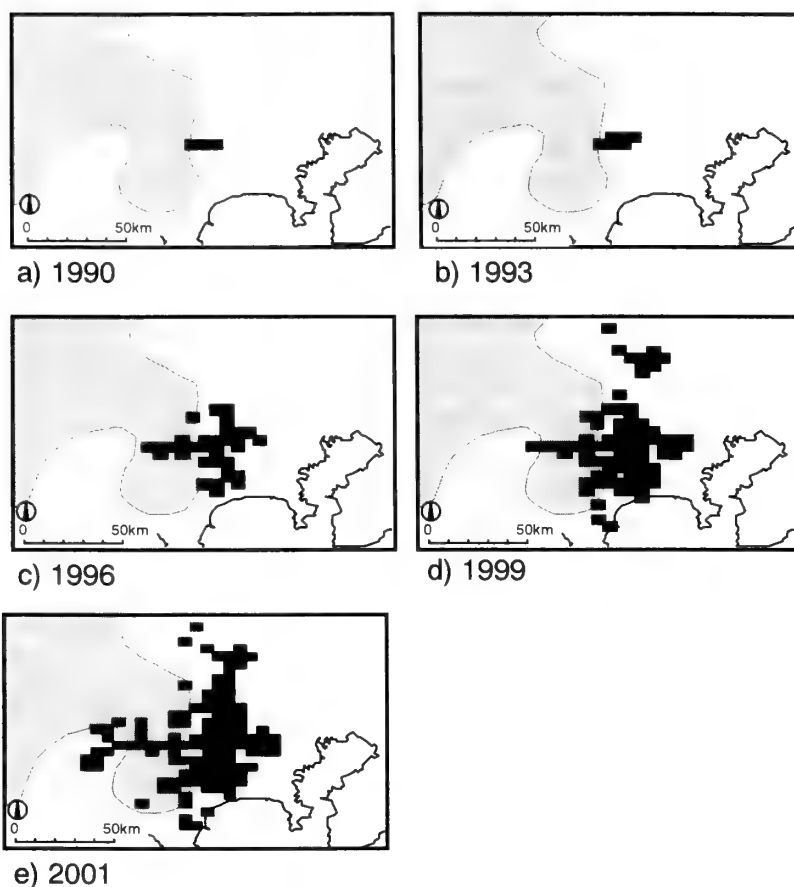


Fig. 3. The distribution of introduced Melodious Laughing Thrushes by year in Western Kanto. The symbol is the same as Fig. 2.

nated in Fukushima City, northern Fukushima Prefecture in 1997, and expanded toward the east and south. By 2001, this population had spread to southern Miyagi and northern Ibaraki prefectures. The Nagano population appeared at Saku City in 1995 and the distribution was restricted to near the city. Although the area was expanded once, it has subsequently decreased.

We excluded the following records from the analysis, because no record was obtained in subsequent years near the site; at Hachioji, Tokyo in 1981; at Sakai City, Osaka in 1994; and at Mt. Tsukuba, Ibaraki in 1998. We also excluded the record from Yasato City, Ibaraki in 2000, because it was far from main populations and could not be classified.

Fig. 6 shows the relationship between the square root of the area of 100% minimum convex polygon occupied by Melodious Laughing Thrushes (y) and the year (x) for each population. The relationships between them are expressed as $y=2.30x-4560$ (a, 1985–1994, $r=0.947$) and $y=3.03x-5990$ (b, 1995–2000,

$r=0.979$) for the Kyushu population, $y=1.29x-2570$ (c, 1987–1993, $r=0.896$) and $y=8.90x-17700$ (d, 1994–2001, $r=0.990$) for the Kanto population and $y=13.4x-26800$ (e, $r=0.959$) for the Tohoku population.

2) Snow depth and elevational conditions

The areas that have more than 20 cm deepest snow depth of normal years (heavy snow area) were shown in Fig. 2–5. There was no heavy snow area near the center of the distribution for the Kyushu population (Fig. 2). At the Kanto population, Melodious Laughing Thrushes extended its range mainly without the heavy snow area. Though the distribution extended across the heavy snow area, the route was along the low elevation area where is considered to have relative light snow (Fig. 3). At the Fukushima population, the distribution seemed to spread avoiding the heavy snow area (Fig. 4). There was a light snow area about 20 km west of the Nagano population, though the species occurred in a heavy snow area

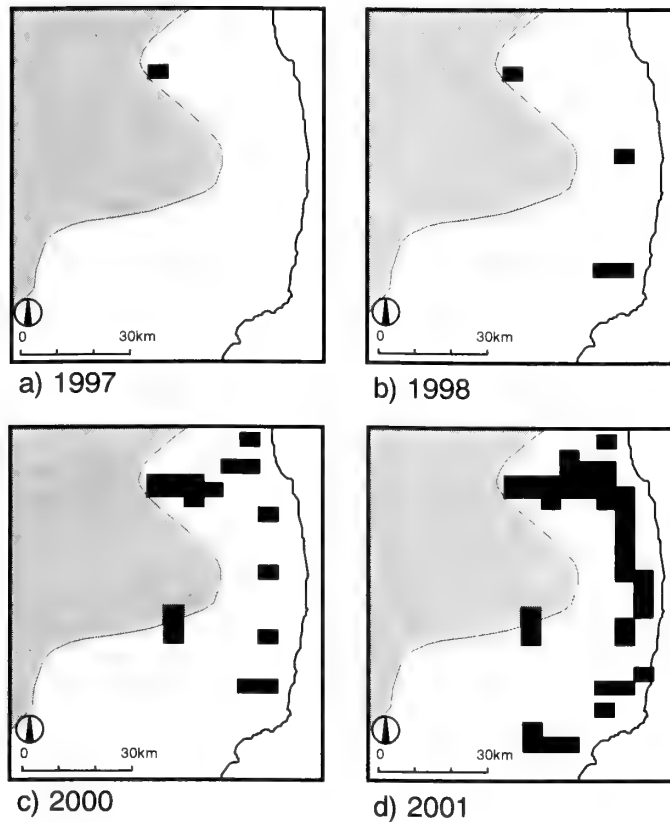


Fig. 4. The distribution of introduced Melodious Laughing Thrushes by year in Southern Tohoku. The symbol is the same as Fig. 2.

(Fig. 5).

There was no record for elevations higher than 1400 m. The ranges of elevations of the four populations were 0–1000 m (Kyushu), 0–1400 m (Kanto), 0–600 m (Tohoku) and 400–800 m (Nagano; Fig. 7).

DISCUSSION

1) Nationwide distribution

There were four populations of Melodious Laughing Thrushes: in northern Kyushu, western Kanto, southern Tohoku and Nagano Prefecture. The oldest information was from 1985 in northern Kyushu, while Sato (2000) noted that the species had already been observed in the early 1980s at Rikimaru Dam in northern Fukuoka Prefecture.

These four populations had discrete origins and occurred discontinuously since the 1980s. The Red-billed Leiothrix *Leiothrix lutea* was also naturalized at various region of Japan since the 1980s, most likely due to releases by individuals and shops (Eguchi 2002). The patterns of distributions were similar between the two species. The same likely oc-

curred with Melodious Laughing Thrushes, though the cause of the naturalization is unclear. One presumable cause of naturalization is the increase of dense understory. This species prefers dense understory as breeding and foraging habitats (Long 1981; Cheng et al. 1987; Sato 2000; Kawakami 2002). In lowland forests, shrub cover has increased and become thicker because of the depression of the forestry industry and insufficient management of rural forests for past few decades (Takeuchi et al. 2001; Forestry Agency 2003). The increase in shrub cover might accelerate the naturalization of this species.

Since the 1980s, four introduced Timalliinae species, i.e. the above two species plus the Masked Laughing Thrush *G. perspicillatus* and the White-browed Laughing Thrush *G. sannio*, have increased in Japan (Nakamura 1993; Eguchi & Amano 1999; Kawakami 2002). These four species and Chinese Bamboo Partridge *Bambusicola thoracica*, which became feral in Japan in the early twentieth century, have similar original distributions, mainly in southern China (China Wildlife Conservation Association

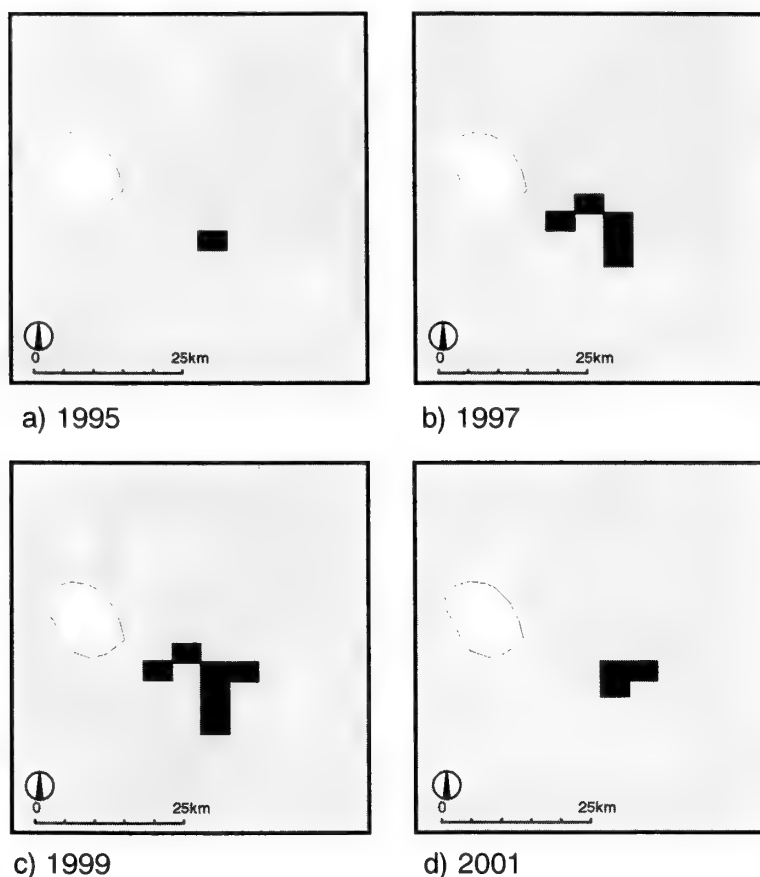


Fig. 5. The distribution of introduced Melodious Laughing Thrushes by year in Nagano Prefecture. The symbol is the same as Fig. 2.

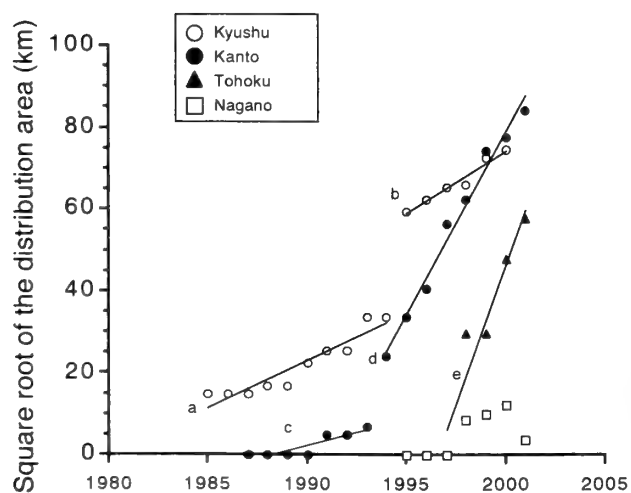


Fig. 6. The square root of the area of 100% minimum convex polygon occupied by Melodious Laughing Thrushes in the four population zones of Kyushu, Kanto, Tohoku and Nagano Prefecture.

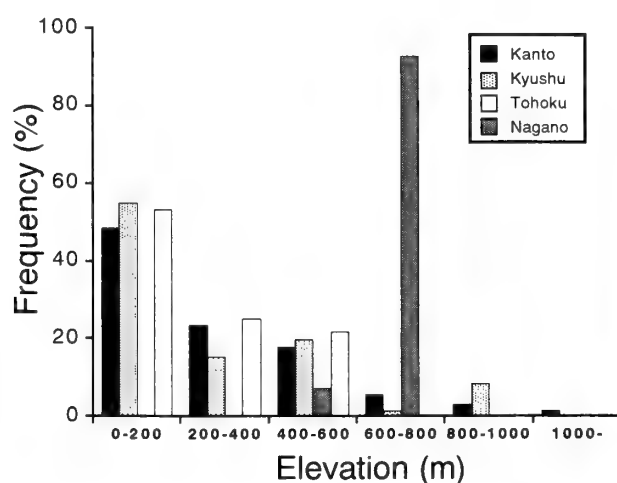


Fig. 7. Elevations of known Melodious Laughing Thrushes habitats. The sample sizes were 218, 71, 14 and 32 for Kanto, Kyushu, Nagano and Tohoku populations, respectively.

1995). There might be a tendency for bird species in this area to naturalize easily in Japanese forests. The environments of original and introduced habitats are considered to be similar, because they belong to the same temperate zone and are geographically close. The conditions might induce these species to naturalize.

The ranges of the species in northern Kyushu, western Kanto and southern Tohoku had been expanding since their occurrences and are considered to be still growing. The expansion rate was initially low but rose subsequently in northern Kyushu and western Kanto. Most introduced species are considered to have establishment period during which they expand their range slowly and expansion period during which they intensively expand (Shigesada 1992). This pattern has been reported for various introduced bird species such as the Common Starling *Sturnus vulgaris* and the House Finch *Carpodacus mexicanus* (Okubo 1988). The pattern of Melodious Laughing Thrushes is considered to be similar as them. The reason why subsequent expansion rate was not so high in northern Kyushu is probably the lack of information, as we could not carry out field observations there. Thus, the actual distribution probably should be wider for 2001. Regarding the Tohoku population, there was no establishment period probably because of lack of initial information. It is probably because of the difficulty to find individuals when the population is small. At western Kanto, we got a typical pattern of expansion, and it likely reflects relative large number of observers in the area.

2) Factors limiting distribution

The distribution in Tohoku and Kanto suggested that the range was limited by the snow depth. Melodious Laughing Thrushes mainly forage on the ground in the non-breeding season (Yamaguchi 2000; Kawakami unpubl.), and they are mainly resident (Long 1981; Mountainspring & Scott 1985). Therefore, it appears that they are not able to inhabit heavy snow areas because the snowfall prevents them from foraging in the non-breeding season.

Near the population in Nagano Prefecture, there was an area of light snow (Japan Meteorological Agency 1993). This suggests that the population was established in an area of comparatively light snow. As the data of the normal years is the average value for latest thirty years (Japan Meteorological Agency 1993), there may be annual variation in snow depth. The snow depth was relatively low in 1998 and 1999

beside the previous years in Nagano Prefecture (Snow Research Center 2003), when Melodious Laughing Thrushes increased. When it was deeper in Nagano Prefecture in 2000 and 2001, the population became smaller (Fig. 6). This finding supports the possibility of that the snowfall limits the distribution.

Snowfall in Japan is considered to have decreased since the 1990s (Japan Meteorological Agency 2002). This trend may have facilitated the establishment of populations in Tohoku district and Nagano Prefecture which usually have heavy snowfall. As global warming has occurred since the last century, it would decrease snowfall hereafter. If so, Melodious Laughing Thrushes will likely expand their range northward.

The distribution was restricted to lowland forests and they mainly occurred at elevations below 1000 meters in all areas. This is consistent with a report on the native population, which mentioned that this species occurs at 0–1500 m (Cheng et al. 1987). This tendency might be caused by the snowfall condition above mentioned, as higher elevational area has relative heavy snowfall. And, there is a possibility that the other ecological factors exclude the species from the higher elevational area, such as poor food resources in winter and the insufficiency of appropriate habitats. At the same time, there is a possibility that underestimation was arisen by the lack of observations at higher elevational area. In order to clarify it, more information is required.

Although Melodious Laughing Thrushes are considered to be resident in principal, there might be a population that shows a degree of movements. There is a possibility that individuals that breed at high elevational area move to lower area in winter at Mt. Tanzawa, Kanagawa Prefecture (Y. Kato pers. comm.). It is necessary to investigate the seasonal vertically movement in detail.

3) Conservation of native forest birds

Some studies have showed that introduced birds tend to select anthropogenic habitats whilst native birds favour forests (Greig-Smith 1986; Moffat & Minot 1994). Most of introduced bird species in Japan were also established at anthropogenic habitats (Eguchi & Amano 1999). Melodious Laughing Thrushes, however, have been found in natural forests (Eguchi & Amano 1999). Thus, there is a concern that the species would have an impact on the population of Japanese native forest birds such as thrushes that utilize the same resources as Melodious Laughing Thrushes (Yamaguchi 2000; Kawakami

2002), like the cases of other introduced species (e.g. Wootton 1987; Jones 1996). Mountainspring & Scott (1985) indicated that Melodious Laughing Thrushes competed with native species and affected their population densities in the Hawaiian Islands. But there has been no study on the impact of this species in Japan.

They have already become one of the commonest birds in lowland forests in the Kanto district (K Kawakami unpubl.). In order to control the population of Melodious Laughing Thrushes, it might be effective to remove the understory vegetation, which this species prefers as habitat (Kawakami 2002). But this measure would also impact native species. Above all things, it is necessary to assess effects of this species on native birds in future studies and provide possible countermeasures before Melodious Laughing Thrushes thrive in Japan.

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Breeding density of exotic Red-billed Leiothrix and native bird species on Mt. Tsukuba, central Japan

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Abstract Exotic Red-billed Leiothrix *Leiothrix lutea* numbers have increased in southern, western and central part of Japan since the early 1980's. Unlike most naturalized birds, this species mainly breeds in natural deciduous forests. We researched the breeding bird density in a deciduous forest on Mt. Tsukuba (877 m), a major breeding area of leiothrix in central Japan, in 1994 and 1995. Leiothrix bred at very high density (350–400 pairs per 100 ha) and was the most dominant species in both years. In 1995, six complete nests were found in a 1 ha area. In spite of the high breeding density of leiothrix, native avifauna showed species diversity, total breeding density and total biomass, similar to other Japanese deciduous forests. Therefore, we suggest that leiothrix have invaded Mt. Tsukuba without severe competition with native bird species.

Key words Breeding density, Interspecific competition, Introduced species, *Leiothrix lutea*, Red-billed Leiothrix

The Red-billed Leiothrix *Leiothrix lutea* is native to Himalayas, Assam, western and northern Myanmar, southern China and northern Vietnam (MacKinnon & Phillips 2000). This species is a popular cage bird and has been introduced successfully into the Hawaiian Islands (Long 1981; Berger 1981; Ralph et al. 1998). Around 1980, breeding populations of leiothrix were found in the southern, western and central parts of Japan and have increased in numbers since then (Eguchi & Masuda 1994, Tojo 1994).

Although many exotic bird species have naturalized in Japan (Ecological Society of Japan 2002), most of them breed exclusively in man-modified habitats. The sole exotic species that invaded Japanese forests by 1970's is the Chinese Bamboo Partridge *Bambusicola thoracica*. This partridge was introduced and released in 1919 and became established in warm temperate areas in Japan (Kiyosu 1978), although its main habitats are dense bushes and cultivated fields, not large forest tracts nor deep mountains. The preferences for man-modified habitats in exotic species are also seen in other countries

and islands. Diamond and Veitch (1981) explored New Zealand avifaunas and concluded that only after decimation of native species and forest alteration by browsing mammals could exotic birds invade forests. On the other hand, Case (1996) examined the global patterns in the establishment and distribution of exotic birds and found that the most important correlates of success of exotic birds is the number of native species extinctions, which reflects the degree of human activity and habitat destruction and deterioration through the introduction of exotic predators, herbivores and parasites.

Unlike earlier avian invaders in Japan, main breeding habitats of leiothrix are natural deciduous forests. In Kyushu, it breeds in beech forests as well as *Tsuga* and *Abies* forests with dense undergrowth above 1000 m in elevation and became the most dominant species in some areas (Eguchi & Masuda 1994, Eguchi & Amano 2000). The successful invasion of leiothrix into Japanese deep forests seems to contradict the general trend and severe competition with native bird species of such natural forests may be expected. Mountainspring and Scott (1985) explored passerine birds associations in native forests in the Hawaiian Islands, which exotic Red-billed Leiothrix,

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Japanese White-eye *Zosteropus japonicus*, and Melodious Laughing Thrush *Garrulax canorus* have invaded, and found that native/exotic species-pairs had a significantly greater proportion of negative partial correlations than either native/native pairs or exotic/exotic pairs. They argued that although the negative correlations were for the most part small, one species could eventually replace another as spatial displacement accumulated through time.

Unfortunately, as monitoring data on avifauna of Japanese forests into which leiothrix have penetrated are not available in most cases, detection of its effects is difficult. However, when the invasion occurred in small, isolated ecosystems, serious effects, including competitive local exclusion, might occur, as Mountainspring and Scott (1985) expected. They also pointed out that if competition occurs between native and exotic species, it seems reasonable to expect it to be most severe during population explosions. Therefore, the rapid increase of leiothrix since 1980's could have caused drastic changes in certain native bird populations; a problem needing study.

In this paper, we research breeding density of the exotic Red-billed Leiothrix and native bird species in an isolated natural deciduous forest in order to document how leiothrix have increased in it. Then, we examine its effects on the native bird community by comparing our census results with an avifaunal list on Mt. Tsukuba before leiothrix invasion and with bird communities of other similar Japanese forests.

STUDY SITE AND METHODS

The study was performed in a deciduous forest on Mt. Tsukuba (877 m, 36°13'N, 140°06'E), a major breeding area of leiothrix in central Japan. Although Mt. Tsukuba is not a high mountain, as it stands between warm-temperate and cool-temperate zone, its natural vegetation changes in relation to altitude, from broad-leaved evergreen forest in lowland area to broad-leaved deciduous forest around the summits. A beech forest, typical cool-temperate forest type in Japan, is the dominant vegetation above 700 m alt. around the two peaks of Mt. Tsukuba. Smaller beech forests also occur at some lower summits within surrounding hill areas (Ibaraki Prefectural Forest Experimental Station 1980; Fukamachi et al. 1996).

While a part of the forest areas on Mt. Tsukuba has been protected by the Tsukuba Shrine and by the Japanese government, it also has been used for tourist industries and public institutions. Tourists can reach

800 m alt. by a cable tramcar or by a ropeway, and many constructions, such as tramcar stations, restaurants, souvenir shops, a climate observatory and an electric wave observatory, have been built between the two peaks. About half of them are concentrated in a small open area named "Miyukigahara". A part of the beech forest was cut about 70 years ago.

The first known record of leiothrix on Mt. Tsukuba was of three individuals in October 1980 (Ishii 1992). Leiothrix breeds in the beech forest around the peaks of Mt. Tsukuba in dense numbers, but probably wanders to lower areas in flocks during non-breeding season, as done in their native range (e.g. Ali 1977). A monthly bird census in a forest on a hillside (300 m alt.) 9 km apart from the main peaks of Mt. Tsukuba showed that leiothrix had increased in number during 1988–1993 and 33 individuals were captured within 2 days in October 1992 (Tojo 1994).

Territory mapping method (Williamson 1964; Bibby et al. 1992) was used to estimate breeding density of birds of the beech forest. We set an 8 ha plot (east-west 400 m, south-north 200 m, about 700–800 m alt.) on the north slope of Mt. Tsukuba. Beech *Fagus crenata*, oak *Quercus crispula*, cherry *Prunus sargentii* are the dominant canopy species. Thick understory growth of dwarf bamboo *Sasamorpha borealis*, which reaches up to 200 cm, is found over most of area. A part of the southern edge of the plot is within 50 m from Miyukigahara and the northern edge is in contact with red pine *Pinus densiflora* stands and Japanese cedar *Cryptomeria japonica* plantations, which are located in lower areas of the northern slope on Mt. Tsukuba. A census route was made so as to come within 50 m of every point on the plot. Ten census trips were carried out from mid April to mid June in both 1994 and 1995. Territory that extended outside the plot was counted as 0.5 pair.

In 1995, we set a 1 ha intensive area within the 8 ha plot and tried to locate all leiothrix nests in it. As we had carried out a banding survey by mist netting, a number of the leiothrix were uniquely colour banded, which helped in identifying territory holders.

As far as we know, there is no quantitative data of avifauna on Mt. Tsukuba before leiothrix invasion, although Haga (1988) prepared a list of birds observed on Mt. Tsukuba during the previous ten years. This includes a period before the first record of leiothrix in 1980. The 76 species listed contains birds seen in the whole area of Mt. Tsukuba throughout the year. We excluded species that were not recorded in the breeding bird census by territory mapping in the

beech forest on Mt. Tsukuba, such as raptors, nocturnal, aerial, aquatic and farmland species (see appendix for details). Breeding status of some short distant migrants on Mt. Tsukuba was difficult to judge. We excluded the Brown Thrush *Turdus chrysolaus* and the Grey-faced Bunting *Emberiza spodocephala*, which might have bred during this period, as well as the Goldcrest *Regulus regulus*, that Haga (1988) described as a "winter visitor, but some records in summer". A list of 35 species remained, that likely to be breeding birds before leiothrix invasion, are compared to our census results.

Another comparison is with similar Japanese forests. Hino (1990) reviewed avifaunal studies in Japanese mature deciduous forests and found that 25–35 species had territories and total densities were about 500 pairs per 100 ha. He selected four studies

that satisfied following criteria: (1) mapping census methods had to be used; (2) forest age had to be at least 100 years; (3) coniferous trees were not a major component of the forests; and (4) the forest area, including census site, had to be large as not to be influenced by surrounding habitats. We compared our results with all the studies that Hino examined except for Nakamura (1983), because it might have used different methods from territory mapping. Instead, we added Nakamura (1986) for the comparison, a census work carried out the same beech forest in Kayanodaira, Nagano Prefecture. We also included Suzuki et al. (1983) and Fujimaki (1988) that generally meet the criteria, although some disturbances occurred within 100 years before the surveys. We compared breeding species number, total breeding density and total biomass presented in these six studies, 3 were from Hokkaido and 3 from Honshu (Fig. 1, Table 1), with those on Mt. Tsukuba. For the body mass of each bird species we referred to Kiyosu (1966) and Dunning (1993). For the studies of two census years, we used means.

RESULTS

1) Territory mapping

Thirty-seven bird species, including exotic leiothrix and the Chinese Bamboo Partridge, were recorded in the plot in the two census years. Twenty-three and 27 species were found to occupy territories in 1994 and 1995, respectively. Leiothrix was the most dominant breeding species, occupying about one third of total territories, in both years (Table 2). For native bird species, Bush Warbler *Cettia diphone* and Great Tit *Parus major* were dominant bird species, occupying 15% and 10%, respectively. Species of which average dominance exceeded 2% were Japanese Pygmy Woodpecker *Dendrocopos*

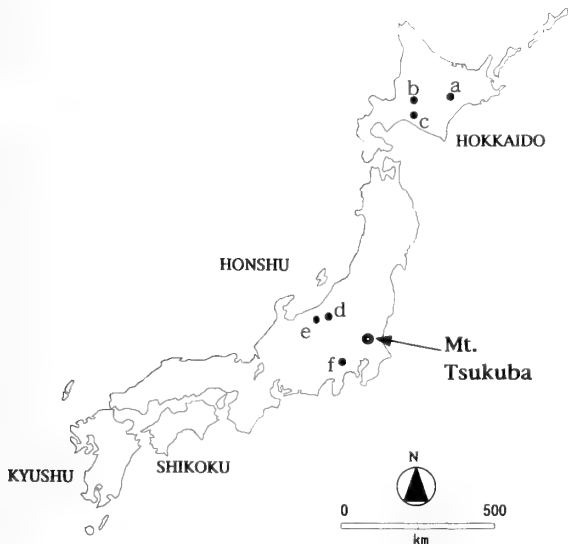


Fig. 1. Location of Mt. Tsukuba and study sites of referred studies. Abbreviations: a; Fujimaki (1988), b; Suzuki et al. (1983), c; Fujimaki (1986), d; Nakamura (1986), e; Mitsuishi (1970), f; Uramoto (1961).

Table 1. Breeding bird surveys by mapping methods in Japanese natural deciduous forests

Source	Prefecture	Plot size	Study years	Altitude (m)	Dominant tree species
Present study	Ibaraki	8 ha	2	700–800	<i>Fagus crenata</i> , <i>Quercus crispula</i> , <i>Prunus sargentii</i>
Fujimaki 1988	Hokkaido	24.75 ha	2	320	<i>Quercus crispula</i> , <i>Prunus sargentii</i> , <i>Lespedeza bicolor</i>
Suzuki et al. 1983	Hokkaido	15.5 ha	2	60–100	<i>Ostrya japonica</i> , <i>Acer mono</i>
Fujimaki 1986	Hokkaido	24.75 ha	2	60	<i>Quercus crispula</i> , <i>Magnolia obovata</i> , <i>Prunus sargentii</i>
Nakamura 1986	Nagano	5.7 ha	1	1460–1500	<i>Fagus crenata</i>
Mitsuishi 1970	Nagano	2986 m*	1	1200–1400	<i>Fagus crenata</i>
Uramoto 1961	Saitama	2750 m*	2	900–1200	<i>Fagus crenata</i> , <i>F. japonica</i>

* Territories were mapped along a census belt with width determined for each bird species.

Table 2. Number of territories in 8 ha plot

Family	Common name	Scientific name	1994	1995
Phasianidae	Chinese Bamboo Partridge	<i>Bambusicola thoracica</i> *	+	+
	Copper Pheasant	<i>Syrnaticus soemmerringii</i>	+	0.5
Columbidae	Rufous Turtle Dove	<i>Streptopelia orientalis</i>	1.0	0.5
	Japanese Green Pigeon	<i>Sphenurus sieboldii</i>		+
Cuculidae	Fugitive Hawk Cuckoo	<i>Cuculus fugax</i>		0.5
	Oriental Cuckoo	<i>Cuculus saturatus</i>	0.5	1.0
	Little Cuckoo	<i>Cuculus poliocephalus</i>	1.0	1.5
Picidae	Japanese Green Woodpecker	<i>Picus awokera</i>	0.5	1.0
	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>	1.5	2.5
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>	2.5	1.5
Laniidae	Bull-headed Shrike	<i>Lanius bucephalus</i>	+	
Troglodytidae	Winter Wren	<i>Troglodytes troglodytes</i>	0.5	1.0
Turdidae	Japanese Robin	<i>Erithacus akahige</i>	+	0.5
	Siberian Blue Robin	<i>Luscinia cyane</i>	1	1.5
	White's Thrush	<i>Zoothera dauma</i>	+	+
	Siberian Thrush	<i>Turdus sibiricus</i>	+	
	Grey Thrush	<i>Turdus cardis</i>	1.0	0.5
	Short-tailed Bush Warbler	<i>Urosphena squameiceps</i>	4.5	3.5
Sylviidae	Bush Warbler	<i>Cettia diphone</i>	13.5	10.5
	Arctic Warbler	<i>Phylloscopus borealis</i>		+
	Eastern Pale-legged Leaf Warbler	<i>Phylloscopus borealoides</i>	+	
	Crowned Willow Warbler	<i>Phylloscopus coronatus</i>	1.0	1.0
	Narcissus Flycatcher	<i>Ficedula narcissina</i>	1.0	1.5
Muscicapidae	Blue and White Flycatcher	<i>Cyanoptila cyanomelana</i>	0.5	1.0
	Brown Flycatcher	<i>Muscicapa dauurica</i>		+
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>	2.0	3.0
Paridae	Willow Tit	<i>Parus montanus</i>	+	1.5
	Coal Tit	<i>Parus ater</i>	1.0	1.5
	Varied Tit	<i>Parus varius</i>	1.5	2.5
	Great Tit	<i>Parus major</i>	8.5	7.5
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>	1.5	3.0
Emberizidae	Siberian Meadow Bunting	<i>Emberiza cioides</i>	0.5	1.0
Fringillidae	Japanese Grosbeak	<i>Eophona personata</i>	1.0	0.5
Ploceidae	Tree Sparrow	<i>Passer montanus</i>		+
Corvidae	Jay	<i>Garrulus glandarius</i>	1.0	1.0
	Jungle Crow	<i>Corvus macrorhynchos</i>	+	+
Timaliidae	Red-billed Leiothrix	<i>Leiothrix lutea</i> *	28.5	33.5
Total number of territories			75.5	85.0
Number of species that occupied territories			23	27

+: presence in the plot without occupying territories.

*: introduced species.

kizuki, Brown-eared Bulbul *Hypsipetes amaurotis*, Short-tailed Bush Warbler *Urosphena squameiceps*, Long-tailed Tit *Aegithalos caudatus*, Varied Tit *Parus varius* and Japanese White-eye. The Siberian Meadow Bunting, an edge species, had territories near Miyukigahara. Tree Sparrows *Passer montanus*, which live almost exclusively in residential areas in Japan and are seen in Miyukigahara year round, were

also recorded in 1995.

2) Density and fates of nests

Six complete nests were found in a 1 ha area of the plot in 1995 (Fig. 2). Of those, four nests contained clutches and one nest contained a broken eggshell. No egg was observed in the remaining one nest, possibly predated soon after laying. Other than the 6

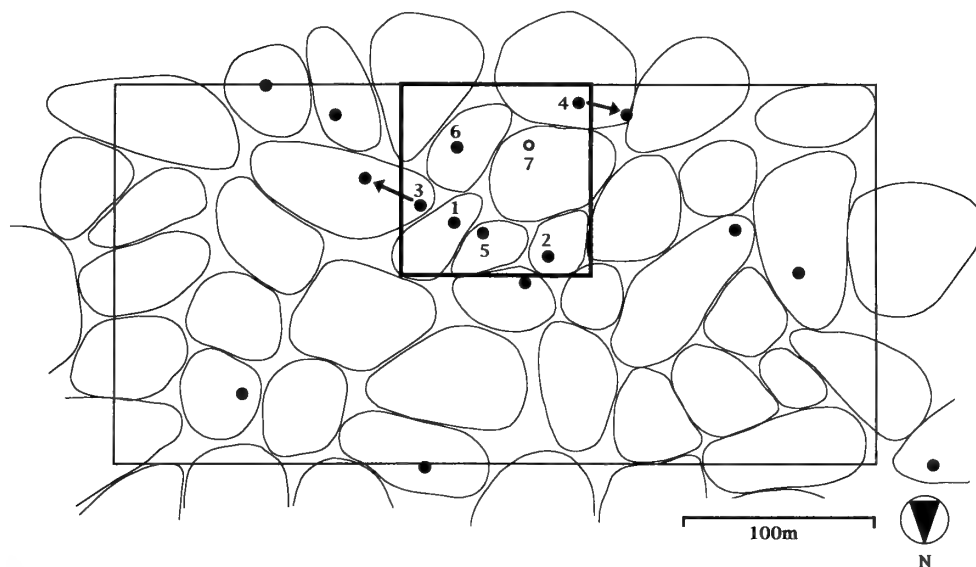


Fig. 2. Distribution of leiothrix territories and nests in 1995. The square shows the 1 ha intensive area for nest survey. Closed circles show complete nests and an open circle shows an incomplete nest. Arrows indicate re-nesting by same males after nest predation.

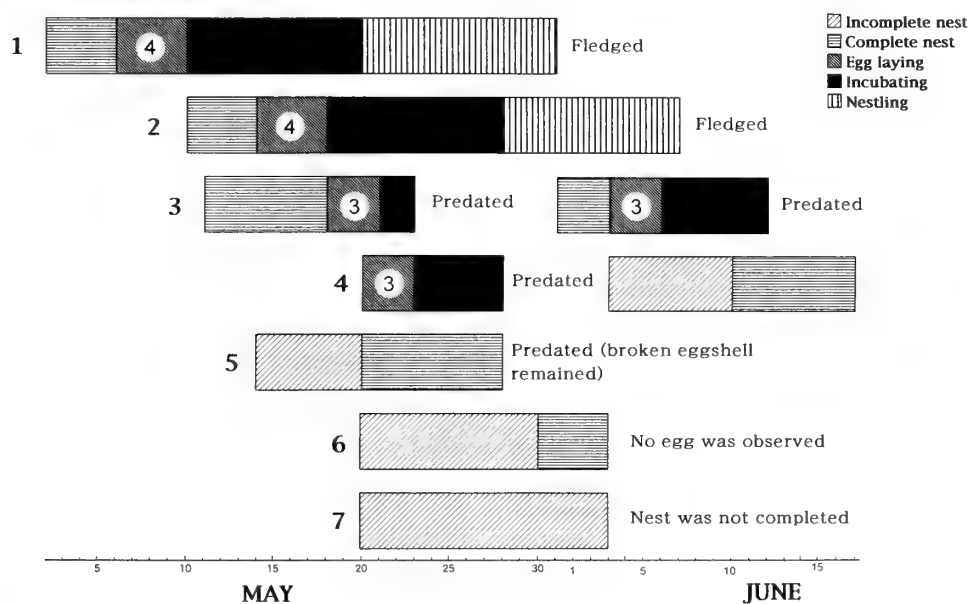


Fig. 3. Stages and fates of leiothrix nests in the 1 ha area in the plot. Numbers of each bar indicate nests in Fig. 2. Numbers in laying periods in bars show clutch size of each nests. Both two replacement nests were outside the 1 ha area.

complete nests, an incomplete nest was found in the 1 ha area. We felt that it were difficult for us to locate all the nests in the dwarf bamboo bushes even within 1 ha area.

All males associated these territories were color banded and two of them re-nested after predation of their nests, though females were not identified in both

cases. Two out of the 6 complete nests in the 1 ha area are supposed to have fledged young, and two ringed young from one nest were recaptured within the breeding season (Fig. 3). Of the four remaining nests, at least 3 nests had predated eggs.

Although leiothrix nest from April to September on Mt. Tsukuba (pers. obs.), the six complete nests

and here were most likely to be first nesting attempts. Therefore, their density would represent minimum breeding density in early breeding season, at least 600 pairs per 100 ha in this case, though sample area is small.

3) Comparison with Haga's list

Our list of birds that were found in the plot lacks Common Cuckoo *Cuculus canorus* and Great-spotted Woodpecker *Dendrocopos major*, which were listed in Haga's list. The Great-spotted Woodpecker is rarely seen on Mt. Tsukuba, but in much smaller numbers than Japanese Green Woodpecker *Picus awokera*, another medium-sized woodpecker. The Common Cuckoo is basically not a bird of forest, although it is rarely heard around Miyukigahara.

We recorded three tropical migrant species, Horsfield's hawk Cuckoo *Cuculus fugax*, Siberian Thrush *Turdus sibiricus*, Pale-legged Warbler *Phylloscopus borealoides* that Haga's list lacks. While latter two species were transients, the Horsfield's hawk Cuckoo, which parasitizes on flycatchers and robins, occupied a territory in 1995.

4) Comparison with other Japanese deciduous forests

The average number of breeding native bird species in the six forests compared was 26.8 (20–32.5, Fig 4 (1)), similar to that on Mt. Tsukuba (24). Mt. Tsukuba lacked Great-spotted Woodpecker and Nuthatch *Sitta europaea*, which bred in all six forests. From Haga's list, it is clear that the Nuthatch was absent on Mt. Tsukuba even before leiothrix invasion. The Japanese Green Pigeon *Sphenurus sieboldii*, White's Thrush *Zoothera dauma* and Brown Flycatcher *Muscicapa dauurica*, which bred in four out of the six forests, did not occupy territories on Mt. Tsukuba, although were present in the plot at least in one study years. In contrast, Japanese White-eye, a common breeder on Mt. Tsukuba, did not occupy territories in the six forests compared.

The breeding density of native birds of Mt. Tsukuba (616 pairs per 100 ha) is in the range of the six previous studies (370–620 pairs, average 505 pairs, Fig. 4 (2)). Including leiothrix, total breeding bird density on Mt. Tsukuba reached around 1000 pairs per 100 ha. The presence of leiothrix, thus, does not seem to depress breeding density of native birds.

Total biomass is markedly affected by presence of some large species such as Copper Pheasant *Syrmatiscus soemmerringii*, which weigh about 1000 g.

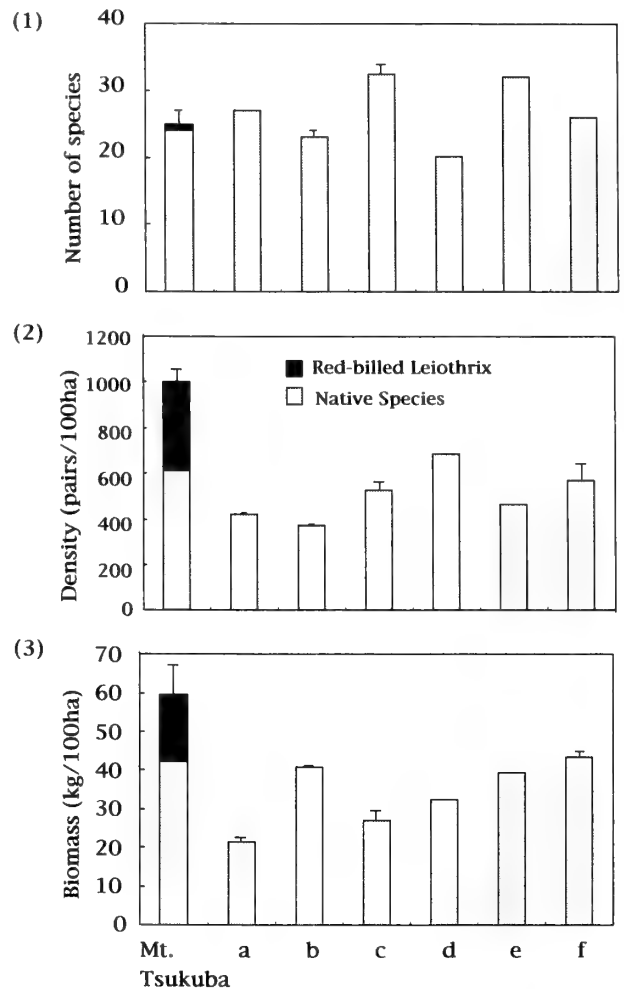


Fig. 4. 1) Number of species 2) total density 3) total biomass of breeding birds on Mt. Tsukuba and in six Japanese natural deciduous forests. See Figure 1 for abbreviations. Bars show SD for data collected in two years.

Again, the biomass of leiothrix (17.5 kg per 100 ha) does not seem to depress that of native birds of Mt. Tsukuba (42.3 kg), which is in the range of the six previous studies (21.5–43.5 kg, average 34.1 kg, Fig. 4 (3)).

DISCUSSION

The territory mapping showed that leiothrix breed in Mt. Tsukuba at a high density, 350–400 pairs per 100 ha, which is comparable to the total breeding bird density reported in some Japanese deciduous forests (e.g. Suzuki et al. 1983; Kobayashi & Fujimaki 1985; Inoue & Kondo 1983). Such a high breeding density is uncommon for Japanese forest bird species, and the sole species comparable to this within the six studies

compared is Coal Tit *Parus ater* in Kayanodaira (Nakamura 1986), which breed at 211 pairs per 100 ha, or at an even much higher density (Nakamura et al. 1987). The nest survey ascertained the high density of leiothrix and even suggested that it may be underestimated. For leiothrix that nest on dwarf bamboo bushes, nest site is less likely to be a limiting factor of breeding density as in many hole nesters (Amano & Eguchi 2002).

It has no doubt that leiothrix have undergone a population explosion peculiar to introduced species since the first record in 1980 on Mt. Tsukuba, although details of the increase are unknown. Haga (1988) wrote that this species was seen in rather large flocks in winter. When we mist-netted in July and September 1990, leiothrix was already the most dominant species. As there were no nearby large leiothrix breeding areas from which mass immigration can occur to Mt. Tsukuba, this rapid increase was caused by successful breeding of the present population.

In spite of the high breeding density of leiothrix, the native avifauna does not seem to be altered. Species that have disappeared in the decade are minimal, if any. The absence, or very low density, of two trunk foragers, Great-spotted Woodpecker and Nuthatch characterizes the avifauna in beech forest on Mt. Tsukuba, but there is little possibility that they have been excluded by leiothrix. Supposed native competitors on Mt. Tsukuba, such as Bush Warbler and Great Tit bred in higher densities than in any of leiothrix-free forests compared in this study. Both total breeding density and total biomass of native species on Mt. Tsukuba are in the range of those in the six compared forests and, therefore, do not seem to be depressed by those of leiothrix.

All-in-all, we did not find any sign of leiothrix impact on native bird species. The total avifauna of Mt. Tsukuba seems to be a simple sum of native species and a huge amount of leiothrix. Therefore, we suggest that leiothrix have invaded Mt. Tsukuba without severe competition with native bird species.

Eguchi and Masuda (1994) found similar results in Kyushu and suggest that leiothrix may have invaded into a vacant niche, a lower layer in the deciduous forests. However, it would be premature to conclude that leiothrix is harmless to native birds. Interspecific competition may have an effect only during infrequent lean periods, as Mountainspring and Scott (1985) suggest. On the other hand, even if leiothrix have lowered breeding success of certain native bird species, breeding density of those species may

change little, because enough recruit may come from surrounding "leiothrix-free" breeding areas for the species. In such cases, however, the effects on breeding density may become apparent when expanding leiothrix breeding area reached a threshold that remaining leiothrix-free breeding areas of the native species no longer produce enough recruits.

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Breeding density of exotic Red-billed Leiothrix and native bird species

Appendix. Avifaunal list on Mt. Tsukuba prepared by Haga (1988)

Family	Compared with present list		Excluded from comparison	
	Common name	Scientific name	* Common name	Scientific name
Ardeidae			c Japanese Night Heron	<i>Gorsakius goesagi</i>
Accipitridae			a Black Kite	<i>Milvus migrans</i>
			a Sparrowhawk	<i>Accipiter nisus</i>
			a Grey-faced Buzzard-eagle	<i>Butastur indicus</i>
			a Kestrel	<i>Falco tinnunculus</i>
Falconidae			b Pheasant	<i>Phasianus colchicus</i>
Phasianidae	Chinese Bamboo Partridge	<i>Bambusicola thoracica</i>		
	Copper Pheasant	<i>Syrnaticus soemmerringii</i>		
Columbidae	Rufous Turtle Dove	<i>Streptopelia orientalis</i>		
	Japanese Green Pigeon	<i>Sphenurus sieboldii</i>		
Cuculidae	Common Cuckoo	<i>Cuculus canorus</i>		
	Oriental Cuckoo	<i>Cuculus saturatus</i>		
	Little Cuckoo	<i>Cuculus poliocephalus</i>		
Strigidae			c Collared Scops Owl	<i>Otus lempiji</i>
			c Brown Hawk Owl	<i>Ninox scutulata</i>
			c Ural Owl	<i>Strix urarensis</i>
Caprimulgidae			c Jungle Nightjar	<i>Caprimulgus indicus</i>
Apodidae			d White-rumped Swift	<i>Apus pacificus</i>
Alcedinidae			e Kingfisher	<i>Alcedo atthis</i>
Picidae	Japanese Green Woodpecker	<i>Picus awokera</i>		
	Great Spotted Woodpecker	<i>Dendrocopos major</i>		
	Japanese Pygmy Woodpecker	<i>Dendrocopos kizuki</i>		
Alaudidae			b Skylark	<i>Alauda arvensis</i>
Hirundinidae			d House Swallow	<i>Hirundo rustica</i>
			d Red-rumped Swallow	<i>Hirundo daurica</i>
			e Grey Wagtail	<i>Motacilla cinerea</i>
Motacillidae			e White Wagtail	<i>Motacilla alba</i>
			e Japanese Wagtail	<i>Motacilla grandis</i>
			g Olive-backed Pipit	<i>Anthus hodgsoni</i>
			f Water Pipit	<i>Anthus spinoletta</i>
Pycnonotidae	Brown-eared Bulbul	<i>Hypsipetes amaurotis</i>		
Laniidae	Bull-headed Shrike	<i>Lanius bucephalus</i>		
Troglodytidae	Winter Wren	<i>Troglodytes troglodytes</i>		
Prunellidae			g Alpine Accentor	<i>Prunella collaris</i>
			g Japanese Accentor	<i>Prunella rubida</i>
Turdidae	Japanese Robin	<i>Erithacus akahige</i>	g Red-flanked Bushrobin	<i>Tarsiger cyanurus</i>
	Siberian Blue Robin	<i>Luscinia cyane</i>	f Daurian Redstart	<i>Phoenicurus aureus</i>
	White's Thrush	<i>Zoothera dauma</i>	g Brown Thrush	<i>Turdus chrysolaus</i>
	Grey Thrush	<i>Turdus cardis</i>	f Pale Thrush	<i>Turdus pallidus</i>
			f Dusky Thrush	<i>Turdus naumanni</i>
Sylviidae	Short-tailed Bush Warbler	<i>Urosphena squameiceps</i>	g Goldcrest	<i>Regulus regulus</i>
	Bush Warbler	<i>Cettia diphone</i>		
	Arctic Warbler	<i>Phylloscopus borealis</i>		
	Crowned Willow Warbler	<i>Phylloscopus coronatus</i>		
Muscicapidae	Narcissus Flycatcher	<i>Ficedula narcissina</i>		
	Blue and White Flycatcher	<i>Cyanoptila cyanomelana</i>		
	Brown Flycatcher	<i>Muscicapa dauurica</i>		
Aegithalidae	Long-tailed Tit	<i>Aegithalos caudatus</i>		
Paridae	Willow Tit	<i>Parus montanus</i>		
	Coal Tit	<i>Parus ater</i>		
	Varied Tit	<i>Parus varius</i>		
	Great Tit	<i>Parus major</i>		

idix. (Continued)

Family	Compared with present list		Excluded from comparison	
	Common name	Scientific name	* Common name	Scientific name
Zosteropidae	Japanese White-eye	<i>Zosterops japonicus</i>		
Emberizidae	Siberian Meadow Bunting	<i>Emberiza cioides</i>	f Rustic Bunting	<i>Emberiza rustica</i>
			g Black-faced Bunting	<i>Emberiza spodocephala</i>
			g Grey Bunting	<i>Emberiza variabilis</i>
Fringillidae	Japanese Grosbeak	<i>Eophona personata</i>	f Brambling	<i>Fringilla montifringilla</i>
			b Oriental Greenfinch	<i>Carduelis sinica</i>
			f Siskin	<i>Carduelis spinus</i>
			f Rosy Finch	<i>Leucosticte arctoa</i>
			f Long-tailed Rosefinch	<i>Uragus sibiricus</i>
			g Bullfinch	<i>Pyrrhula pyrrhula</i>
			f Hawfinch	<i>Coccothraustes</i> <i>coccothraustes</i>
Ploceidae	Tree Sparrow	<i>Passer montanus</i>		
Sturnidae			b Grey Starling	<i>Sturnus cineraceus</i>
Corvidae	Jay	<i>Garrulus glandarius</i>	b Azure-winged Magpie	<i>Cyanopica cyana</i>
	Jungle Crow	<i>Corvus macrorhynchos</i>	b Carrion Crow	<i>Corvus corone</i>
Total number of species			35	41

* reasons for exclusions: a: raptors, b: farmland species, c: nocturnal species, d: aerial species, e: aquatic species, f: not breed in central Japan, g: breed in higher altitudinal areas.

Australasian bird invasions: accidents of history?

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Abstract Exotic bird introductions to Australia, New Zealand and surrounding islands, have been aggregated into one of the best documented and most completely analysed datasets available on biological invasions. Of the >242 species introduced by Europeans to Australasia during the 18th–20th centuries, at least 32% established long-term viable populations. A review of the literature reveals the most robust predictors of introduction success to be total number of individuals liberated, and the number of separate attempts at introduction. Using generalized linear modelling on a combined regional dataset, I confirm this result, and demonstrate that together these two characteristics of historical introductions correctly explains the observed outcome in 89.3% of cases in Australasia. Further, I show that a simple stochastic population dynamics model, derived for a sub-set of 44 species from entirely independent long-term studies, is also able to achieve a high degree of predictive success (83%). Finally, a suite of meta-analyses have shown the strongest life history and environmental correlates of introduction success to be large body size, low propensity to migrate, climatically matched habitats across the native and invasive geographical range, sexually monochromatic plumage, dietary generalism, and greater behavioural flexibility. The collective results of these analyses on Australasian introductions provide a potentially powerful framework for predicting the probable outcomes of future bird invasions worldwide.

Key words Australia, Biological invasions, Bird introductions, Life history, New Zealand

The historical introduction of exotic birds to Australasia (Australia, New Zealand, New Guinea, and surrounding islands) represents what is almost certainly the most completely documented (Thompson 1922; Long 1981; Newsome & Noble 1986; Lever 1987; Blackburn & Duncan 2001a) and thoroughly analysed (e.g. Diamond & Veitch 1981; Veltman et al. 1996; Duncan 1997; Green 1997; Sorci et al. 1998; Duncan et al. 1999; Legendre et al. 1999; Sol & Lefebvre 2000; Cassey 2001b; Duncan et al. 2001; Forsyth & Duncan 2001; Moulton et al. 2001; Duncan & Blackburn 2002) source of empirical information and natural experiments on invasibility available anywhere in the ecological literature (Kolar & Lodge 2001; Duncan et al. 2003). Bird introductions to the Australasian realm were associated closely with the expansion of European settlement in the 19th century and the formation of ‘acclimatization societies’ (dat-

ing from the 1860s), whose primary goal was to establish a variety of “beneficial or desirable species” in the newly settled lands (Thompson 1922). The main reasons for introducing birds into Australasia are summarized by Long (1981): (i) aesthetics (e.g. European birds were considered superior songsters to native species), (ii) for food, hunting and sport (usually game birds such as pheasants and ducks), (iii) as biological pest control agents (especially sparrows, starlings and mynas), and (iv) accidentally, as escapees from cages or transport vessels.

Invasions by exotic species present a major risk to biodiversity at a global scale (Vitousek et al. 1997; Duncan et al. 2003), yet, paradoxically, commonly increase the biodiversity of ecological communities at local scales (Lodge 1993; Sax et al. 2002). For instance, New Zealand’s avifauna has suffered substantial extinctions in the past, but thanks to the second highest number of attempted bird introductions on any landmass (after Hawaii: Long 1981), now supports a more greater diversity of species (albeit, less

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distinctive) than at any other time in its past (Wilson 1997; Cassey 2001a; Sax et al. 2002).

About 60% of the bird species introduced to Australia and New Zealand originated from the Palaearctic and Australasian biogeographic realms (Duncan et al. 2003). Globally, introductions of birds have been highly non-random with respect to both taxonomic composition and the locations of sources and destinations (Blackburn & Duncan 2001a; Cassey 2002). Of the approximately 9672 extant bird species, about 213 (2%) have been transported by humans and established successfully outside their natural geographic ranges (Cassey 2002), although the number of failed attempts is considerably higher (perhaps as many as 90% for all invasive species; Williamson 1996, and at least 50% for birds; Blackburn & Duncan 2001b). Fewer still of the established species have become widespread and abundant in their naturalized ranges (Duncan et al. 2003). The taxonomic bias in introductions is obvious: over two thirds of worldwide avian invasives come from just 6 of the 145 bird families (i.e. Anatidae, Columbidae, Fringillidae, Passeridae, Phasianidae, and Psittacidae; Blackburn & Duncan 2001a). Australasia ranks 8 out of 11 geographical regions in terms of ease of invasibility (Blackburn & Duncan 2001b), but nevertheless represents approximately 20% of the total documented count of global bird introductions (Blackburn & Duncan 2001a).

Due to the often highly negative impacts of introduced species on the environment, we need to have better predictability of invasion success. Recognised stages of invasion are transport, introduction, establishment, a lag period during which abundances remain low and distribution restricted, spread, and subsequent ecological and human impacts (Kolar & Lodge 2001; Sakai et al. 2001). A key requirement for developing a robust predictive framework from which to understand these processes and potential to intervene to inhibit invasion lies in the identification and ranking of factors which, under a range of circumstances, predispose particular species or groups to being successful (or failed) invaders of new lands (Williamson 1996). These factors can be broadly categorized as acting at the level of the species (e.g. life history traits), location (e.g. environment at the introduction site) and event (e.g. number of individuals released) (Blackburn & Duncan 2001b; Duncan et al. 2003). Detailed empirical data are available for these factors on the bird introductions of Australasia, thereby providing an ideal case-study of natural ex-

periments from which to develop and test the theory of invasion ecology (Kolar & Lodge 2001).

MAJOR DETERMINANT OF INVASION SUCCESS—INTRODUCTION EFFORT

The most consistent and powerful predictor of invasion success for birds in Australasia has been shown repeatedly to be introduction effort by humans—both in terms of the number of individual birds released (often termed ‘propagule pressure’), and the number of separate attempts at release (see Newsome & Noble 1986; Veltman et al. 1996; Duncan 1997; Green 1997; Duncan et al. 1999; Blackburn & Duncan 2001a; Duncan et al. 2001; Duncan et al. 2003). Similarly strong relationships have been found when examining large mammal and insect invasions (see Daehler & Strong 1993; Forsyth & Duncan 2001 and references cited therein).

There are a number of obvious explanations for this pattern. Stochastic hazards associated with very small population size, such as demographic stochasticity, genetic deterioration, and other “Allee effects” which act to reduce reproductive success at low densities (Shaffer 1981), are offset as founder population size increases (Pimm et al. 1993; Ryan & Siegfried 1994; Green 1997; Legendre et al. 1999; Forsyth & Duncan 2001). Multiple introductions of a given species may provide a demographic ‘rescue effect’, and act to supplement genetic diversity, thereby circumventing problems like inbreeding depression and loss of adaptive fitness associated with population size bottlenecks (Sakai et al. 2001). In addition, some species (e.g. many game birds), had high failure rates because of human hunting pressure (Long 1981; Duncan et al. 2001), poisoning, non-human predation, and lack of suitable habitat (Duncan & Blackburn 2002), which never permitted them to establish large enough resident populations to remain viable over the long-term.

The minimum adequate statistical model developed by Green (1997) to explain establishment success for a sub-set of New Zealand land birds included only propagule size, whilst Cassey’s (2001b) results supported the additional inclusion of number of release events, and geographical range size of a species in their native realm (the latter factors being associated with a higher likelihood of finding matching habitats in newly invaded regions). Precisely this same, three-factor model, was arrived at by Duncan et al. (2001) using independent data for Australian

bird introductions, after having controlled for phylogeny. A lack of migratory tendency was substituted for range size for New Zealand passeriforms (Duncan 1997), and likewise for all New Zealand birds by Veltman et al. (1996). The latter's model explained 97.4% of the variance in introduction success for the 79 species they examined. Supporting these similarities, Sol (2000) found no difference in establishment success for birds invading continental Australia versus New Zealand.

To better understand the degree to which individual components of introduction effort could explain establishment success of exotic birds across the entire scope of Australasia, I used generalized linear modelling (logistic regression), supported by information-theoretic model selection, to re-analyse the combined datasets of Newsome & Noble (1986), Veltman et al. (1996), and Duncan et al. (2001), yielding $N=131$. My modelling framework considered the total number of individuals released [N], number of release events [E], and an interaction term [I], calculated as $N \times E$. Individual species were classed as successful (code=1) or unsuccessful (code=0). For this simple analysis, I deemed it unnecessary to control for phylogenetically-related statistical non-independence (Harvey & Pagel 1991), because compared to life history/ecological correlates (see next section), introduction effort by humans is likely to be only weakly biased taxonomically (Blackburn & Duncan 2001a; Cassey 2002). The Akaike Information Criterion, corrected for small sample size (AIC_c) was used as an objective means of regression model selection, based on considerations of both predictive power and parsimony (detailed in Burnham & Anderson 2002).

The most parsimonious model for predicting invasion success included only number of release events [E], $G=65.6$, $df=1$, $P<0.0001$, Concordance=86.9% (see Table 1 for complete model-selection statistics). However, the fully-specified model also received considerable support from the data (ranked 3/7 overall), $G=67.7$, $df=3$, $P<0.0001$, and explained more of the variance ($C=89.3\%$), the equation being:

$$\text{Invasion success (P)} = 1/[1 + 1/\exp(1.27 \times \log_{10}[N] + 6.73 \times \log_{10}[E] - 1.36 \times \log_{10}[N \times E] - 5.34)] \quad (1)$$

A goodness of fit test on equation (1) revealed no significant deviations from the assumptions of a logistic generalized linear model ($\chi^2=102.1$, $df=97$, $P=0.342$), and no over-dispersion of variance

Table 1. Model selection results, relating likelihood of successful invasion by exotic birds in Australasia (i.e. percentage of introduced species which establish viable populations in Australia and/or New Zealand) to the log-transformed total number of individuals released [N], the log-transformed number of release events [E], and an interaction term [I], calculated as $N \times E$. Model selection criteria are the maximized log-likelihood [$\log(L)$], number of parameters (K ; includes regression intercept and coefficients), information criterion (AIC_c), difference from best model (Δ_i), and Akaike weight (w_i).

Model	$\log(L)$	K	AIC_c	Δ_i	w_i
E	-52.13	2	108.3	0.0	0.444
$N+E$	-51.79	3	109.8	1.4	0.219
$N+E+I$	-51.04	4	110.4	2.1	0.159
$E+I$	-52.12	3	110.4	2.1	0.156
I	-55.48	2	115.1	6.7	0.016
$N+I$	-55.44	3	117.1	8.7	0.006
N	-60.25	2	124.6	16.3	0.000

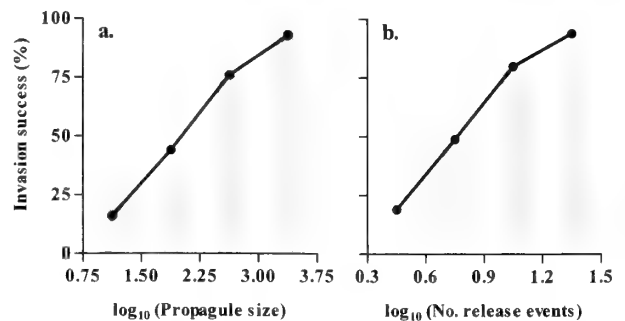


Fig. 1. Relationship between likelihood of successful invasion by exotic birds in Australasia (i.e. percentage of introduced species which establish viable populations in Australia [$n=52$] and New Zealand [$n=79$]) to **a.** total number of individuals ('propagules') released and **b.** number of release (introduction) events. Fitted lines were derived using logistic regression (models ' N ' and ' E ' of Table 1, respectively).

($\hat{c}=1.05$). Thus (unsurprisingly), the strong explanatory power of introduction success holds when taken across the region, but interestingly, the number of release events, not the propagule pressure, was identified by information-theoretic model selection as being the single most important component of invasion success.

EVOLUTIONARY, LIFE HISTORY AND ENVIRONMENTAL CORRELATES

After factoring out the very strong influence of introduction effort on establishment success (i.e. the 'accidents of history'), an obvious question arises:

Do any worthwhile explanatory power remain for life history and environmental attributes of invasive bird species, and if so, which ones? Whilst comparisons among taxa cannot in themselves determine causation, such correlations can at least provide insight into causes, and highlight potential evolutionary influences that are related to variability in introduction success (Cassey 2002). Kolar and Lodge (2001) found a remarkably high number of potential correlates of invasion success (68) had been evaluated across all species in the literature they reviewed. Those traits associated with increased introduction success tended to be related (directly or indirectly) to increases in adult survival and high rates of reproduction, the ability to tolerate or thrive in human modified landscapes, and previous success at invasion (see also Diamond & Veitch 1981; Case 1996; Williamson 1996). Below I present a brief overview of the meta-analyses on ecological correlates which are of most relevance to bird introductions in Australasia. The major correlates examined were geographical range size, migratory tendencies, habitat and dietary generalism, competitive ability, behavioural flexibility, and surrogates for population dynamics, such as body mass and clutch sizes.

Blackburn & Duncan (2001a) showed that species chosen for introduction tended to be abundant in their native range, were hence presumably easy to obtain, and were therefore collected and released in greater numbers. Certain groups in particular, such as wildfowl and other game birds, were chosen preferentially for introduction. Blackburn and Duncan (2001a) and Duncan et al. (2001) were concerned that because species common in Europe also tend to possess life history traits that distinguish them from less abundant species, species-level traits may be confounded by event-level effects such as introduction effort. However, recent work by Cassey (2002) showed no correlation between habitat generalism and geographic range, implying there is little support for the idea that generalist species enjoy high success rates simply because they are more abundant.

Australia's exotic birds show a high proportion of ground nesters which prefer grazing, cultivated, and urban landscapes, and feed predominantly upon seeds and fruit (Newsome & Noble 1986). Conversely, Duncan et al. (2001) found no evidence to support the hypothesis that species with faster reproductive traits, non-migratory, or gregarious behaviour, increased introduction success in Australia. The latter results may be rationalized when one considers that

those traits associated with increased introduction success may be quite different from those which promote successful transportation (Kolar & Lodge 2001), or long-term persistence subsequent to establishment (Duncan et al. 2003). For example, *r*-selected traits (e.g. rapid development, high reproductive potential, short generation intervals, and often weak intra-specific competition) may favour rapid expansion from small founder size (Sakai et al. 2001), but their often concomitantly higher inherent natural population variability also leave such species more prone to local extinction (Pimm et al. 1993). These confounding attributes can result in often confusing or apparently contradictory results when evaluating correlates of introduction success, especially if one relies on studies of fully naturalized birds (Cassey 2001b; Duncan et al. 2001).

Introduction success in New Zealand was lower for species with dichromatic plumage and more generalist diets. The former result may be due to a reduction in 'invasion fitness' caused by higher levels of intra-specific sexual selection pressures (McLain et al. 1999), making such taxa more vulnerable to environmental fluctuations and inter-specific competition, more visible to predators, and reducing their genetically effective population size (Sorci et al. 1998). Behavioural flexibility, such as the ability to rapidly adjust cognitive processes to suit new environments (measured by relative brain size, after controlling for allometry and phylogeny) is another possibility. Species with larger brains and a greater number of documented feeding innovations were shown by Sol and Lefebvre (2000) to be superior invaders.

Ecologists commonly regard extrinsic forces, such as inter-specific competition, as an important determinant of community construction and stability. This idea motivated studies such as Moulton et al. (2001), who provided evidence that competition between alike species, measured by morphological over-dispersion, might contribute to introduction success. This embraces the long-held view that species-rich communities are harder to invade than species-poor ones, because less realized niche-space is presumably available for exploitation (Elton 1958; Holway & Suarez 1999). Analyses examining the success of introduced passeriform birds to New Zealand (Duncan 1997), revealed a pattern which could be explained by either introduction effort or by competition, but Duncan also suggested that morphological over-dispersion might more parsimoniously be explained by the propensity of acclimatization societies to put

greater effort into introducing bird species with a wide diversity of characteristics rather than concentrating on only a few, similar taxa. In support of this conclusion, Duncan and Blackburn's (2002) critique of Moulton et al. (2001) showed that most morphologically similar game bird species would, in most instances, never have had the opportunity to interact or compete with alike species during the early phase of establishment. Similarly, Case (1996) failed to identify a global link between invasion success and species richness of the native avifauna.

THE GLOBAL CONTEXT OF BIRD INVASIONS

Australasian trends tend to be mirrored at the global level. In a comprehensive meta-analysis of worldwide bird introductions, Blackburn and Duncan (2001b) examined 1,466 introduction events for 398 bird species, and, after accounting for introduction effort, showed the probability of invasion success was higher if only a small difference existed between the latitude of origin and latitude of introduction, when introductions were matched with suitable environments, and when range and population size in native regions is comparatively large (see also Blackburn & Duncan 2001a; Duncan et al. 2001), but equally, uncovered no consistent relationship with biotic resistance (whereby species-rich areas such as the tropics were equally easy to invade as more species-poor, temperate and island areas), body mass, generation time, or population growth rate.

Cassey (2002) found that increased habitat generalism, lack of migratory tendency, and sexual monochromatism together explain significant variation in the successful establishment of land birds worldwide. Further, increasing female body weight, and lack of migratory tendency, could together explain 76% of the variation in introduction success among families (see also Cassey 2001a). Parasites are often filtered out as a result of the population size bottlenecks associated with the invasion process (Sakai et al. 2001), and can lead to a demographic release, as apparently occurred for Common Starlings (*Sturnus vulgaris*) introduced into North America (Torchin et al. 2003). In Southeast Asia (the biogeographical division in closest proximity to Australasia), correlates of invasibility included commensalism with humans, facultative colonial nesting, communal roosting, possession of a crop, and ability to congregate rapidly at ephemeral food sources (Lim et al. 2003; Yap & Sodhi 2004).

Phylogenetic effects accounted for an average of 2.1% of the variation in trait values within families for global bird introductions, and 4.7% across families (maximum of 24%), and are therefore surprisingly weak (Cassey 2002).

INVASION SUCCESS AND POPULATION DYNAMICS

Clearly, the probability of successful invasion of Australasia and elsewhere by exotic birds correlates with both introduction effort and certain life history attributes, and this knowledge can be combined to provide a robust phenomenological framework for predicting the probably outcome of future invasion attempts (Daehler & Strong 1993; Kolar & Lodge 2001; Cassey 2002). But on a more fundamental, mechanistic level, what is the population dynamical basis for such predictions? In an attempt to provide a preliminary answer to this question, I undertook the following analysis.

I first extracted long-term population time-series data from the Global Population Dynamics Database (hereafter GPDD, see Inchausti & Halley 2001), from which sufficient information was available to characterize the population dynamics of 44 of the bird species introduced to Australia or New Zealand. For each species, I then fitted a simple stochastic model of exponential population growth via maximum likelihood estimation:

$$\ln(N_t/N_{t+1}) = r + z\sigma_r \quad (2)$$

where N is the population size at time t , r is the intrinsic rate of population increase, σ_r is the standard deviation of r , and z is a standard normal distributed random deviate (Barker & Sauer 1992; McCallum 2000; Morris & Doak 2002). A list of the species and associated parameter estimates are given in Table 2. Finally, a stochastic simulation representation of equation (2) was implemented in Microsoft® Excel, and used to estimate, for each species separately, the initial population size at which the likelihood of establishment of a given species was >50%. This process is analogous to estimating a minimum viable population size in conservation biology (sensu Shaffer 1981; Ryan & Siegfried 1994; Reed et al. 2003), except that the aim in this case is to determine the number of founders required for a species to be more likely invade successfully than to fail.

This population dynamics modelling approach predicted successfully the observed outcome in 54 of 65

Table 2. Predictions of invasion success for exotic birds in Australia and New Zealand, using a simple population dynamics model of stochastic exponential growth. A sub-set of 44 species was used, for which long-term and independent population time-series data was available to parameterize the model. The actual outcome was predicted correctly by the model (indicated by a * in the columns labeled 'I') in 83% (54/65) of individual cases.

Scientific name	q	r	σ_r	Predicted N (model)	Australia			New Zealand		
					I	N	E	I	N	E
<i>Aix sponsa</i>	14	-0.022	0.149	529	—	—	—	0*	10	5
<i>Alauda arvensis</i>	47	0.045	0.331	23	1*	526	13	1*	391	11
<i>Alectoris rufa</i>	14	-0.037	0.177	2,478	0*	9	1	0*	20	2
<i>Anas acuta</i>	48	-0.036	0.236	2,693	—	—	—	0*	102	3
<i>Anas penelope</i>	18	-0.070	0.798	846,754	—	—	—	0*	32	5
<i>Anas platyrhynchos</i>	48	-0.003	0.141	85	1*	86	4	1*	1,539	17
<i>Anser anser</i>	9	0.042	0.129	13	—	—	—	0*	7	2
<i>Anser caerulescens</i>	28	0.069	0.117	12	—	—	—	0*	10	1
<i>Aythya fuligula</i>	36	0.032	0.280	29	—	—	—	0*	5	2
<i>Branta canadensis</i>	21	0.000	0.168	51	0*	4	2	1*	60	10
<i>Callipepla californica</i>	23	0.024	0.600	146	—	—	—	1*	1,420	15
<i>Carduelis cannabina</i>	20	0.046	0.222	47	0*	32	4	0	209	12
<i>Carduelis carduelis</i>	14	0.066	0.193	10	1*	223	5	1*	626	14
<i>Carduelis chloris</i>	16	-0.061	0.432	74,139	1	133	7	1	65	6
<i>Carduelis flammea</i>	20	0.106	1.374	503	—	—	—	1*	607	10
<i>Carduelis spinus</i>	20	0.012	1.081	6,297	0*	80	3	0*	54	3
<i>Colinus virginianus</i>	46	-0.013	0.400	507	—	—	—	1*	1,156	17
<i>Corvus frugilegus</i>	13	-0.074	0.192	183,187	—	—	—	1	182	10
<i>Corvus monedula</i>	15	0.214	0.218	4	—	—	—	0*	3	2
<i>Cygnus olor</i>	116	0.006	0.077	50	1	12	5	1	29	6
<i>Emberiza citrinella</i>	20	-0.043	0.490	12,941	0*	34	3	1	656	14
<i>Emberiza schoeniclus</i>	20	0.027	0.415	46	—	—	—	0*	9	2
<i>Erithacus rubecula</i>	29	0.001	0.188	170	0*	47	3	0*	123	11
<i>Fringilla coelebs</i>	26	-0.029	0.509	3,500	0*	498	4	1	449	17
<i>Fringilla montifringilla</i>	20	-0.020	0.409	1,000	0*	78	1	0*	121	7
<i>Lagopus lagopus</i>	32	0.044	0.919	387	—	—	—	0*	4	2
<i>Luscinia megarhynchos</i>	34	0.010	0.246	49	0*	4	1	0*	7	4
<i>Passer domesticus</i>	26	0.029	0.726	215	1*	414	20	1*	416	12
<i>Perdix perdix</i>	140	0.003	0.767	1,444	0*	4	2	0*	676	24
<i>Phasianus colchicus</i>	30	0.062	1.265	1,531	1	750	12	1	244	27
<i>Pluvialis squatarola</i>	21	0.090	0.179	8	—	—	—	0*	3	2
<i>Prunella modularis</i>	30	-0.045	0.386	10,066	—	—	—	1	245	14
<i>Pyrhula pyrrhula</i>	26	0.029	0.540	62	0*	14	1	0*	12	2
<i>Streptopelia turtur</i>	12	-0.058	0.674	146,902	0*	8	1	—	—	—
<i>Struthio camelus</i>	13	0.081	0.741	42	1*	500	4	—	—	—
<i>Sturnus vulgaris</i>	41	0.070	0.452	20	1*	292	9	1*	653	14
<i>Sylvia atricapilla</i>	26	-0.024	0.521	2,533	—	—	—	0*	5	1
<i>Sylvia communis</i>	20	0.001	0.147	66	—	—	—	0*	2	1
<i>Tetrao tetrix</i>	40	0.029	0.453	49	—	—	—	0*	13	2
<i>Turdus merula</i>	26	0.018	0.327	46	1*	102	8	1*	596	16
<i>Turdus philomelos</i>	26	0.067	0.532	28	1*	129	8	1*	343	12
<i>Tympanuchus phasianellus</i>	20	0.137	0.732	29	—	—	—	0*	22	1
<i>Tyto alba</i>	14	-0.031	0.410	2,777	—	—	—	0*	7	1
<i>Vanellus vanellus</i>	47	-0.040	0.544	12,595	—	—	—	0*	124	8

Definitions: q =years of time-series data, r =intrinsic rate of increase, σ_r =standard deviation of r , I=invasion outcome (0= failure, 1= success), N =total number of individuals introduced, E =number of release (introduction) events.

Data sources: q , r , and σ_r are derived from the GPDD (<http://cpbnts1.bio.ic.ac.uk/gpdd/>); I, N and E are given in from Long (1981), Veltman et al. (1996), Green (1997), and Duncan et al. (2001).

cases involving these species (83%; see Table 2) - a considerably better result than the 50% success rate expected by chance ($G=30.7$, $df=1$, $P<0.0001$), despite there being a number of simplistic postulates associated with equation (2), e.g. the lack of demographic stochasticity or negative feedbacks, and the assumption of a globally consistent value for r and σ , across all environments of a species. The reason this semi-mechanistic model predicts invasion success so well is probably because: (i) a suite of relevant life history variables is effectively collapsed into its two basic parameters (Dennis et al. 1991; Morris & Doak 2002), and (ii) it represents such a fundamental and robust framework for population ecology, from which most other more complex models are derived (Turchin 2001). A good example in point is the case of the European Partridge (*Perdix perdix*), which failed to establish in New Zealand, despite enjoying at least 24 attempts at introduction with a total of 676 individuals being liberated. This failure vexed Veltman et al. (1996), but is in fact predicted correctly by the population dynamics model, being very likely a product of the species' high level of inherent population variability (Pimm et al. 1993).

IMPACT AND MANAGEMENT OF EXOTIC BIRDS IN AUSTRALASIA

Exotic birds now comprise a substantial element of Australasia's avian biota, especially in urban, agricultural and other human-dominated landscapes (Cayley 1973; Kentish et al. 1995; Martin 1996; Pell & Tidemann 1997a). For example, whilst a survey of resident bird species in suburban Melbourne recorded only 9 of 43 species as being invasives, these few species were extremely abundant, representing over two-thirds (69%) of 2,856 sightings (Green 1984). Similarly, introduced Common Mynas (*Acridotheres tristis*) reach densities exceeding 120 birds km^{-2} in suburban Canberra, and are continuing to increase (Pell & Tidemann 1997a).

The environmental, agricultural and concomitant economic impact of invasive birds is a substantial global problem—Pigeons (*Columba livia*) and Starlings alone have been estimated to cost the United States economy over \$US1,900 million annually in damage and control costs (Pimentel et al. 2000). Australasia faces comparable problems from naturalized exotic birds (Bomford & Sinclair 2002), including: damage to fruit crops (cherries, blueberries, grapes, olives) by Starlings, Blackbirds (*Turdus merula*),

House Sparrows (*Passer domesticus*), and Mynas; spreading of noxious weeds (Starlings and Blackbirds); as vectors of human and livestock disease (Starlings and Sparrows); impacts on intensive cattle, pig and poultry production (which rely on high grain rations) by Starlings, Sparrows and Pigeons; defacing of buildings and as hazards to public amenities (by all of the abovementioned species); and perhaps of most concern, their often detrimental interactions with native bird species (including direct and indirect competition for feeding and breeding resources, and genetic introgression) by Starlings, Mynas, Blackbirds, House Sparrows, Javan Sparrows (*Lonchura oryzivora*), Nutmeg Manikins (*Lonchura punctulata*) and Mallards (*Anas platyrhynchos*), and interference with, or predation upon, other taxa, such as arthropods, fish and mammals (for details, see Long 1981; Green 1984; Kentish et al. 1995; Martin 1996; Pell & Tidemann 1997b; Bomford & Sinclair 2002).

Even given these realized and potential impacts of invasive bird species, it is usually argued that the economic and logistical resources devoted to their management and control fall far short of being proportional to the risks involved (Pimentel et al. 2000; Bomford & Sinclair 2002). Successful, scientifically-based management, requires an inherently interdisciplinary endeavour, involving ecology, economics, and mathematics. If combined effectively, an intellectually diverse approach can help to both determine realistic environmental goals, and evaluate the effectiveness of methods to arrive at these targets (Leung et al. 2002). For instance, the successful and on-going control of invasive House Crows (*Corvus splendens*) and Mynas (*Acridotheres* spp.) in Singapore owes its success to an integrated management programme involving governmental support, scientific monitoring, population and statistical modelling, direct on-ground actions such as shooting, and indirect activities such as habitat manipulation, and public education campaigns (see Yap et al. 2002; Brook et al. 2003; Lim et al. 2003).

NEW FRONTIERS

Without adequate management and control efforts, the problems associated with exotic birds are likely to increase in the future, because many invasive bird populations in continental Australia have probably not yet had sufficient time since colonization to reach an ecological equilibrium. For instance, the Common Myna, House Sparrow and Starling continue to ex-

... their distributional ranges within Australia (Long 1981; Newsome & Noble 1986; Martin 1996), and are already beginning to invade ever further into the continent's tropical regions (McCrie 2000). Eurasian Tree Sparrows (*Passer montanus*) have also entered the continent as far north as Darwin, but have to date been quickly identified and eradicated. This leaves the feral Pigeon as the only exotic bird currently resident in northern Australia, although efforts are underway (e.g. shooting, restriction of homing pigeon licences) to attempt to eliminate this species too (Chapman 2000).

In New Zealand, however, the situation may be less worrisome. Duncan et al. (1999) have shown that the contemporary geographic range size of introduced birds does not depend on the length of time since they were introduced, but instead reflected primarily the extent and availability of preferred habitat (see also Diamond & Veitch 1981), suggesting that range expansion after initial founding events was rather rapid (within 50 years), and has reached equilibrium (carrying capacity) for most species. In other words, in this region at least, things have probably already got as bad as they are ever likely to get, unless authorities and the populace relax their vigilance to permit deliberate or accidental introductions.

CONCLUSION—ACCIDENTS OF HISTORY?

A synthesis of historical, ecological, genetic, behavioural and evolutionary perspectives is essential for predicting the introduction success and subsequent spread of invasive species (Sakai et al. 2001)—a point exemplified by the wealth of analyses published on the introduction of exotic birds to Australasia. Although has been claimed that invasion success is largely unpredictable and case-specific (Lodge 1993; Williamson 1996), recent results (e.g. Veltman et al. 1996; Duncan et al. 2001) show that patterns of success and failure, during and after introduction, are indeed highly predictable, provided key species- location- and event-level attributes are known. The frequent failure of life history traits to explain adequately establishment success in non-Australasian birds examples may simply reflect the universal and overriding importance—but generally severely constrained knowledge of—introduction effort and environmental matching (Duncan et al. 2003). The post-release spread and proliferation of introduced species also appears to include a component of historical circumstance (Duncan et al. 1999), whereby species

with larger contemporary range sizes were also those that benefited from the greatest introduction efforts, and were therefore able to exclude competitively later arrivals by sheer predominance in the landscape (Duncan et al. 2003)—truly 'accidents of history'.

The collective results of these quantitative, empirically-grounded analyses on Australasian bird introductions, provide a potentially powerful framework for predicting the likelihood of success of future avian invasions throughout the world, as well as making valuable contributions to development of environmental management policy. For example, the existing insights regarding propagule size and frequency of release events are sufficient to inform guidelines for maximum individual holdings or total populations of exotic birds held in captivity. Research into establishment patterns of invasive birds also has the potential to make valuable contributions to predictive ecology in general; for instance, quantifying the importance (and magnitude) of propagule size and number of events is likely to be informative for reintroduction programmes of threatened species (Green 1997), and may help advance our understanding of the ecological rules of community assembly (Kolar & Lodge 2001).

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Invasive birds in Hong Kong, China

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Abstract The natural vegetation of Hong Kong is tropical evergreen forest, but this was almost entirely cleared by people before the eighteenth century. This clearance must have had a major impact on the bird community and undoubtedly caused the disappearance of all forest-dependant species, but these changes are undocumented. The documented history of Hong Kong's avifauna begins following British colonization in 1860 and parallels a process of progressive restoration of forests, at least in the uplands. At least nine bird species that were present in Hong Kong in 1860 are dependant upon anthropogenic habitats and are therefore considered to have invaded before colonial times. Subsequently 41 species (30% of the breeding avifauna) have colonized. Of these, 22 species are believed to have spread unaided from southern China, while the remaining 19 species are considered to have been introduced by people from sources both within and beyond the region. Unlike the pattern of documented bird invasions elsewhere in Southeast Asia, most of these recent invaders are forest species, reflecting the recent pattern of habitat change. The possible ecological impacts of these invaders (both natural and human-assisted) are reviewed, but they are largely unknown. Hong Kong may provide a model for the evolution of bird communities elsewhere in the region if current patterns of deforestation are permitted to continue.

Key words Birds, Exotic species, Invasions, Tropics

The Hong Kong Special Administrative Region of the People's Republic of China (hereafter, Hong Kong) is a biogeographically arbitrary 1100-km² section of coastal southern China, along with the adjacent islands (Fig. 1) (Dudgeon & Corlett 1994). The landscape of southern China has been so greatly modified by human impacts that any attempt to reconstruct its natural state is inevitably speculative to some degree. The whole region has a forest climate, with hot wet summers and cool dry winters. Moreover, it forms part of a continuous belt of forest climates stretching from the tip of the Malay Peninsula in the south to the arctic tree-line in the north, with no significant barriers to dispersal apart from the south-north climatic gradient. One important point in this gradient—the line between frost-free and frost-prone environments—runs through Hong Kong, but this is much more significant for plants than birds (Dudgeon & Corlett 1994). Hong Kong's natural veg-

etation would have been tall, species-rich, tropical evergreen forest, but less tall, less species-rich and less evergreen than forests nearer the equator. Natural open habitats in the Hong Kong region must have been rare, with coastal cliffs and beaches, and per-

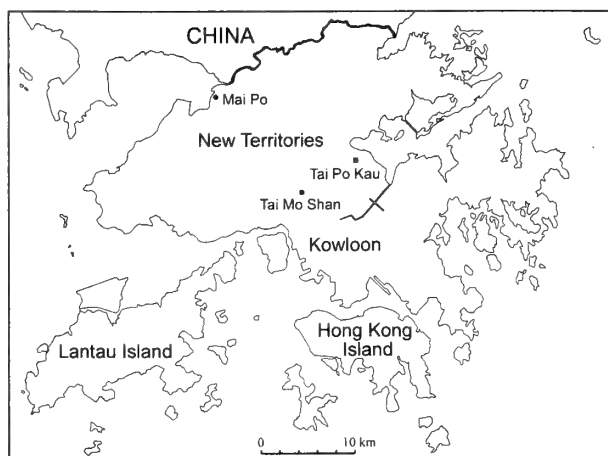


Fig. 1. Map of Hong Kong showing the places mentioned in the text.

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... seasonally flooded riverine grasslands, the only ones extensive enough to support non-forest birds.

Although early human settlements in the region must have had some impact on the biota, the major period of deforestation—leading eventually to the total transformation of the landscape of southern China—seems to have started following increased Chinese immigration in the eleventh and twelfth centuries (Marks 1998). The process accelerated with population increases in the sixteenth and seventeenth centuries, and was essentially completed by the end of the eighteenth century. There are no descriptions of Hong Kong itself before the mid eighteenth century, but earlier European visitors to the Pearl River delta region, west of Hong Kong, make no mention of forest (Corlett 1997). Historical settlement patterns in Hong Kong suggest that deforestation proceeded from the coast inland and from the lowlands upwards. Even the highest slopes were terraced for tea by the late seventeenth century—probably earlier—and it is hard to see where any substantial area of forest could have survived in Hong Kong past this date.

The words “bleak”, “barren” and “bare” appear in all nineteenth century descriptions of the Hong Kong (Dudgeon & Corlett 1994). The lowlands were almost entirely under cultivation, while the uplands were mostly grassland, maintained by fires and the cutting of hillside biomass for fuel. Forest cover survived during this period of maximum human impact as *feng shui* woods near villages, as linear patches along upland streams, and as small stands in topographically protected sites (Zhuang & Corlett 1997). None of these forest patches is likely to have been big enough to support populations of forest-dependent birds, even without the additional impacts from hunting and trapping (Corlett 2000). The absence from Hong Kong of forest pheasants, resident woodpeckers, most of the expected babblers, and a range of other forest species presumably dates from this period. The human population of Hong Kong is now approaching 7 million. Agriculture has been largely abandoned and the lowlands are being rapidly urbanized. By contrast, the intensity of human impact in upland areas has declined. Shrubland and secondary forest are replacing the fire-maintained grasslands (Zhuang & Corlett 1997) and more than half the non-urban area is under some form of legal protection (Dudgeon & Corlett 1994).

The situation in Hong Kong is thus very different from that in most of Southeast Asia (Wells 1999). The ecological transformation that is occurring cur-

rently in Southeast Asia, as forest is being replaced by a variety of non-forest habitats, occurred at least 300 years ago in Hong Kong (Corlett 2000). The loss of bird species from isolated and degraded forest fragments that is just starting in Southeast Asia (Wells 1999; Brook et al. 2003) has gone almost to completion in Hong Kong, where the expanding secondary forests are dominated by habitat generalists and new arrivals of various origins (Kwok & Corlett 1999, Corlett 2000).

Hong Kong may be the future of Southeast Asia—we hope not!—but it is also a place without an ecological history. Bird records go back only to 1860, when Robert Swinhoe visited Hong Kong (Swinhoe 1861), and anything before that is partly speculation. This complete absence of a pre-impact baseline is a major problem for many kinds of ecological research in Hong Kong. For invasive birds, the problem is somewhat less, as most of the obvious introductions have occurred in the last few decades, but it is still difficult to determine which of the bird species present in 1860 would have been present prior to deforestation and which are actually early invaders. We also face a further difficulty in that, alongside the recent documented introductions of obviously exotic bird species, Hong Kong is experiencing colonization by a suite of species that are native to southeast China. All of these may have been present in Hong Kong's primeval forests, though we cannot be certain of this. Some of these species have reached Hong Kong naturally, but for others there is strong evidence that the populations have been introduced. Accordingly, in assessing the impact of invasive bird species, we have divided our review into two periods: the period before 1860 for which there are no historical records (Table 1) and the period since. In this second period, we have distinguished between those species which appear to have colonized (or recolonized) Hong Kong naturally (Table 2) and those that appear to have been introduced by human agency (Table 3).

SPECIES PRESENT IN 1860

The nine species listed in Table 1 are all wholly or largely associated with anthropogenic habitats in Hong Kong. All are widespread in southern China (Cheng 1987; Lewthwaite 1996) and Hong Kong (Carey et al. 2001). Two species (Eurasian Tree Sparrow and Common Magpie; bird scientific names are in the Tables) have a wide distribution in the Palearctic Region (Clements 2000) and it seems probable

Table 1. Species known to be present in Hong Kong prior to 1860 which are solely or largely restricted to anthropogenic habitats.

Species in this and the following Tables have been ascribed to feeding guilds as follows: C=carnivore, F=frugivore, G=granivore (including seed predators and herbivores), I=insectivore, N=nectarivore and O=omnivore. For some species, distributions within Hong Kong are distinguished as HKI (Hong Kong Island) or NT (New Territories).

Species English Name	Species Scientific Name	Feeding guild	Anthropogenic habitats utilised (in approximate order of importance)	Natural habitats utilised
Spotted Dove	<i>Streptopelia chinensis</i>	G	Farmland, urban, urban fringe, fishponds, grassland with shrubs.	—
Oriental Magpie Robin	<i>Copsychus saularis</i>	I	Farmland, urban fringe, urban, fishponds.	Mangroves.
Masked Laughingthrush	<i>Garrulax perspicillatus</i>	I/F	Urban fringe, farmland, fishponds, grassland with shrubs.	—
Scaly-breasted Munia	<i>Lonchura punctulata</i>	G	Farmland, fishponds, grassland, shrubland.	—
Eurasian Tree Sparrow	<i>Passer montanus</i>	G	Urban, urban fringe, farmland, fishponds.	—
Black-collared Starling	<i>Sturnus nigricollis</i>	O	Farmland, fishponds, urban fringe, urban.	—
White-shouldered Starling	<i>Sturnus sinensis</i>	I/F	Farmland, fishponds, coastal shrubland, urban fringe.	—
Crested Myna	<i>Acridotheres cristatellus</i>	O	Farmland, fishponds, urban, urban fringe, coastal shrubland.	—
Common Magpie	<i>Pica pica</i>	O	Farmland, fishponds, urban, urban fringe, shrubland, grassland.	—

that they have reached Hong Kong and southern China from the north, as has previously been suggested for the Eurasian Tree Sparrow (Summers-Smith 1988). A further three species (Spotted Dove, Oriental Magpie Robin and Scaly-breasted Munia) have widespread distributions in the Oriental Region (Clements 2000). These three species are widespread in Hong Kong, although Scaly-breasted Munias are absent from urban areas (Carey et al. 2001). Spotted Doves and Scaly-breasted Munias are restricted to anthropogenic habitats, but Oriental Magpie Robins are common in mangroves and it has been suggested that this is the original habitat of the species in this region (Carey et al. 2001). The distributions of the remaining four species (Masked Laughingthrush, Black-collared Starling, White-shouldered Starling and Crested Myna) are largely restricted to southern China (Clements 2000), so they are presumably native to this region, but in Hong Kong they are restricted to habitats that are wholly anthropogenic in origin (Leven 2000; Carey et al. 2001). Although we have no information on the pre-1860 bird trade or bird release practices, the continuity of suitable anthropogenic habitats between Hong Kong and the probable source areas of the ten species means that all these species could have reached Hong Kong as natural colonists, without direct human assistance.

NATURAL COLONISTS SINCE 1860

Forty-one species have become established as breeding birds in Hong Kong since 1860 (Tables 2 & 3) (Kershaw 1904; Herklots 1967; Chalmers 1986; Carey et al. 2001). Twenty-two species are considered to have reached Hong Kong without direct human agency (Table 2), though some are dependent on anthropogenic habitats. The other 19 species (Table 3) are believed to have populations founded by individuals that were released by humans. Separation into the two categories has been based on review of the pattern of establishment, together with an assessment of the natural vagility of the species and the proximity of potential source populations (Carey et al. 2001, pp 108–113). Characteristics considered likely to be indicative of natural colonists include: species with potential source populations in South-east China; species known to be migratory or irruptive with a pattern of a progressive increase in records of transient individuals prior to the establishment of a breeding population; species where the first Hong Kong populations became established in the northern New Territories (i.e. near the border with the rest of China); and species that are relatively infrequent in the cage bird trade. Conversely, the patterns of colonization of species considered likely to have been introduced by humans show one or more of the following features: species not occurring naturally in

Table 2. Species that have colonized Hong Kong since 1860 without direct human agency.

Species English Name	Scientific Name	Diet	Breeding habitats	Pattern of invasion	Reasons for invasion
Black Baza	<i>Aviceda leuphotes</i>	I/C	Forest	Increasing summer visitor from 1972; now stable in low numbers.	Forest maturation, perhaps natural range expansion in China.
Black-winged Kite	<i>Elanus caeruleus</i>	C	Famland, wetlands	Irregular throughout the year from 1984; has bred, still rare and probably not established.	Range expansion in China.
Crested Serpent Eagle	<i>Spilornis cheela</i>	C	Forest	First recorded 1940, gradual increase from 1950s, further increase in 1980s & 90s. Now widespread in NT.	Forest maturation.
Crested Goshawk	<i>Accipiter trivirgatus</i>	C	Forest	Pre 1980s status confused, but undoubted increase since.	Forest maturation.
Besra	<i>Accipiter virgatus</i>	C	Forest	Pre 1990s status confused, probable increase since 1980s.	Forest maturation.
Emerald Dove	<i>Chalcophaps indica</i>	G	Forest, shrubland	First recorded 1960, widespread (but low density) from 1980s.	Forest maturation.
Chestnut-winged Cuckoo	<i>Clamator coromandus</i>	I	Forest, shrubland	First recorded 1957 but rare until c. 1980, subsequent rapid increase.	Spread of Greater Necklaced Laughingthrush (host).
Hodgson's Hawk Cuckoo	<i>Hierococcyx fugax</i>	I	Forest	One record 1971, annual since 1994.	Forest maturation? Spread of host?
Little Swift	<i>Apus affinis</i>	I	Widespread but only breeds in urban areas	First recorded 1941, colonized during 1950s, now in all urban areas.	Nest site availability?
Great Barbet	<i>Megalaima virens</i>	I/F	Forest, NT only	1920s, widespread by 1950s (HKI colonized 1930s–1960s then died out).	Forest maturation.
White Wagtail	<i>Motacilla alba</i>	I	Wetland, farmland, urban	Sporadic breeding species until 1990s, rapid increase, now common and widespread.	Unknown.
Grey-chinned Minivet	<i>Pericrocotus solaris</i>	I	Forest	First record 1957, first in summer 1981, first proven breeding 1984, continued increase and spread in 1990s (NT only).	Forest maturation.
Scarlet Minivet	<i>Pericrocotus flammeus</i>	I	Forest	First record 1950, first in summer 1975, subsequent gradual increase and spread central NT.	Forest maturation.
Chestnut Bulbul	<i>Hypsipetes castanonotus</i>	I/F	Forest	First recorded 1936, increased in 1960s but largely as winter visitor, regular breeding during 1980s, continued spread since.	Forest maturation.
Orange-bellied Leafbird	<i>Chloropsis hardwickii</i>	I/F/N	Forest	One record 1934, otherwise since 1984, first breeding 1989, gradual spread in 1990s.	Forest maturation, probable natural spread but some evidence of human introduction.

Table 2. (Continued).

Species English Name	Scientific Name	Diet	Breeding habitats	Pattern of invasion	Reasons for invasion
Orange-headed Thrush	<i>Zoothera citrina</i>	I/F	Forest	First recorded 1956, sporadic until 1980s, then gradual increase, still rare.	Forest maturation.
White-bellied Yuhina	<i>Yuhina zantholeuca</i>	I/F	Forest	First recorded 1980, subsequent slow increase and spread.	Forest maturation, probable natural spread but could be derived from human introduction.
Hainan Blue Flycatcher	<i>Cyornis hainanus</i>	I	Forest	First recorded 1958, gradual subsequent spread (perhaps more rapidly in 1990s).	Forest maturation.
Buff-bellied Flowerpecker	<i>Dicaeum ignipectus</i>	I/F	Forest	First recorded 1954 but perhaps previously overlooked, undoubted increase from 1960s, breeding from 1975, continuing gradual increase.	Forest maturation.
Fork-tailed Sunbird	<i>Aethopyga christinae</i>	I/N	Forest, parks, urban fringe	First recorded 1959, slow increase during 1960s, rapid since 1970s, now common and still spreading.	Forest maturation, ornamental tree planting?
White-rumped Munia	<i>Lonchura striata</i>	G	Forest, shrubland, urban	First recorded 1913 but scarce and irregular until 1970, then rapid increase and spread.	Unknown, widely traded and breeding population may have, at least, been have, at least, been bolstered by released birds.
Large-billed Crow	<i>Corvus macrorhynchos</i>	O	Farmland, wetlands, open country, urban fringe	First recorded 1934, progressive spread through HK (from North) reaching HKI by 1950s, numerical increase since.	Unknown.

Southeast China; species not known to be naturally migratory or irruptive; a relatively sudden appearance of a breeding population with few prior observations of transients; initial population foci in or near urban areas or on Hong Kong Island; birds showing physical or behavioral evidence of former captivity; and species occurring frequently in trade (Leven 2000; Carey et al. 2001). For most species, we can be confident that their assignment to either Table 2 or Table 3 is correct, though for some, the evidence is not overwhelming either way. In addition, for at least one species not included in Tables 2 and 3, White-rumped Munia, the pattern of records suggests that both natural colonization and large-scale Buddhist releases

have occurred (Vaughan & Jones 1913; Webster 1976; Carey et al. 2001).

The overwhelming majority (18 out of 22) of the species that are considered to be natural colonists occur in forest or shrubland and their establishment in Hong Kong since 1860 presumably reflects the expansion of these habitats over this period (Zhuang & Corlett 1997; Corlett 1999; Corlett 2000). Most are insectivores or insectivore/frugivores. Most insectivores and many insectivore/frugivores which breed in Southeast China are migratory or irruptive (Cheng 1987; Lewthwaite 1996), doubtless because of the marked seasonality of food availability (Kwok & Corlett 1999; Leven 2000; Kwok & Corlett 2002)

4. Species that have become established in Hong Kong since 1860 through human agency.

Species English Name	Scientific Name	Feeding guild	Breeding habitats	Pattern of invasion	Possible reasons for invasion
Rock Dove	<i>Columba livia</i>	G	Urban, farmland	Poorly documented, present by 1953, widespread in urban and rural areas, no known change in status since.	Released cagebirds and/or farmed birds.
Yellow-crested Cockatoo	<i>Cacatua sulphurea</i>	G	Urban parks, urban fringe forest HKI only	First in 1960s. Population c. 150—slow increase.	Released cagebirds (extralimital species).
Rose-ringed Parakeet	<i>Psittacula krameri</i>	G	Urban parks HKI (formerly also farmland NT)	First in 1903–1913; population now <20 birds, formerly 100+.	Released cagebirds (extralimital species).
Red-whiskered Bulbul	<i>Pycnonotus jocosus</i>	I/F	Urban, farmland, grassland, forest fringe	Apparently not present 1860, common in 1904, no subsequent change.	Probably human agency (not necessarily in HK).
Streak-breasted Scimitar Babbler	<i>Pomatorhinus ruficollis</i>	I/F	Forest, shrubland	Single records 1949, 1978. Rapid spread since 1986 with foci on HKI and central NT.	Released cagebirds but facilitated by availability of suitable habitat.
Rufous-capped Babbler	<i>Stachyris ruficeps</i>	I	Forest, shrubland	First recorded 1985, rapid spread in 1990s.	Released cagebirds but facilitated by availability of suitable habitat.
Chinese Babax	<i>Babax lanceolatus</i>	I/F	Montane forest, shrubland	First recorded 1959 then small population established on TMS (above c 650 m). No recent change.	Released cagebirds.
Greater Necklaced Laughingthrush	<i>Garrulax pectoralis</i>	I/F	Forest, shrubland	First recorded 1969. Slow spread in 1970s and 1980s, rapid and accelerating in 1990s.	Released cagebirds but facilitated by availability of suitable habitat.
Black-throated Laughingthrush	<i>Garrulax chinensis</i>	I/F	Forest, shrubland	First recorded 1913, but not recorded again until 1950s when found to be widespread on HKI, scattered reports from NT in 1980s, increase and spread in 1990s.	Released cagebirds. Recent spread facilitated by availability of suitable habitat?
White-browed Laughingthrush	<i>Garrulax sannio</i>	I/F	Shrubland, farmland	First record from Cheung Chau (1941), released birds HKI 1961, widespread records from mid-1970s, decline during 1990s.	Released cagebirds.
Silver-eared Mesia	<i>Leiothrix argentauris</i>	I/F	Forest, shrubland	One record 1970, many from 1987, widespread and rapid increase in 1990s.	Released cagebirds (extralimital species).

Table 3. (Continued).

Species English Name	Scientific Name	Feeding guild	Breeding habitats	Pattern of invasion	Possible reasons for invasion
Red-billed Leiothrix	<i>Leiothrix lutea</i>	I/F	Forest, shrubland	Inrequent records from V&J (1913) on but marked upsurge during late 1980s and early 1990s, then marked subsequent decline.	Released c. agebirds.
Blue-winged Minla	<i>Minla cyanouroptera</i>	I/F	Forest	First recorded 1992, rapid subsequent increase.	Released cagebirds (extralimital species).
Vinous-throated Parrotbill	<i>Paradoxornis webbianus</i>	I/G	Montane shrubland, dwarf bamboo above 650 m	First recorded 1971, breeding on TMS from 1980 where small population persists.	Released cagebirds.
Yellow-cheeked Tit	<i>Parus spilonotus</i>	I	Forest	First recorded 1988, widespread records from 1989, numbers peaked early 1990s then declined.	Released cagebirds.
Velvet-fronted Nuthatch	<i>Sitta frontalis</i>	I	Forest	First recorded 1989, limited spread in 1990s, now stable?	Released cagebirds
Baya Weaver	<i>Ploceus philippinus</i>	G	Wetlands	First recorded 1993, breeding confirmed in 1995. Population of c. 30 birds still present.	Released cagebirds (extralimital species).
Common Myna	<i>Acridotheres tristis</i>	O	Farmland, fishponds, villages	First recorded 1952. Regularly recorded since mid-1950s, population fluctuating but small (c. 100 birds).	Released cagebirds (extralimital species).
House Crow	<i>Corvus splendens</i>	O	Urban, container port	First recorded 1974, 12 records by 1998, recent increase to c. 100 birds.	Probably ship-assisted (extralimital species).

and are thus pre-adapted to find and utilize newly available habitat.

The remaining four species (Black-shouldered Kite, Little Swift, White Wagtail and Large-billed Crow) are all associated with open country habitats. As such, their colonization of Hong Kong in the last 50 years or so perhaps represents a continuation of the pattern of spread in southern China of species that are dependent on anthropogenic habitats detailed in Table 1. We have direct evidence of such spread in southern China in the case of Black-winged Kite, which now occurs throughout Southeast China (MR Leven pers. obs.) despite its being considered by Cheng (1987) to be rare and largely restricted to the southwestern Provinces of Yunnan and Guangxi.

HUMAN INTRODUCTIONS SINCE 1860

Nineteen species are considered to have become established in Hong Kong through human agency (Table 3). Apart from the House Crow, which most probably arrived on a ship as it has done in many other parts of the world (Madge & Burn 1994; Ryall 2002), all these species are thought to have been brought to Hong Kong as cagebirds. Some wild populations may have been established by escaped birds, but deliberate releases, usually by Buddhists, are more likely to include multiple individuals of the same species. Other possible reasons for releasing birds include bird dealers getting rid of diseased or surplus stock or, in the case of the parrots, pet owners tiring of the responsibility of looking after long-lived and noisy pets. These 19 species fall into two sub-groups: those which do not occur naturally in south-

China; and those which are native to southeast China, but for which there is evidence that the Hong Kong populations are not of natural origin.

The first sub-group includes nine species: Rock Dove, two parrots (Rose-ringed Parakeet and Yellow-crested Cockatoo), two babblers (Silver-eared Mesia and Blue-winged Minla), Velvet-fronted Nuthatch, Baya Weaver, Common Myna and House Crow. Rock Doves are now widespread in Hong Kong and occur in both urban and rural areas. Presumably, they were introduced to Hong Kong as domesticated birds at some time after the establishment of the colony by the British in 1842. However, the history of this species is obscure and the earliest reference to its presence appears to be that of Webster and Phillipps (1967) by which time it was already widespread. Though Rose-ringed Parakeets were present in Hong Kong from at least 1913 (Vaughan & Jones 1913) and flocks of up to 87 birds were recorded throughout the territory during the 1970s and 1980s, the population declined substantially subsequently and is now restricted to a limited urban area on Hong Kong Island (Carey et al. 2001). Yellow-crested Cockatoos were first noted in Hong Kong in 1961 (Viney 1973) and numbers increased to an estimated at 60–100 birds during the late 1990s and at least 150 birds in 2003 though the population remains largely restricted to the urbanised north side of Hong Kong Island (Carey et al. 2001; MR Leven pers. obs.).

Both Silver-eared Mesias and Blue-winged Minlas have become established in forest and shrubland, the former since 1987 and the latter since 1992 and both species appear to be spreading rapidly in these habitats (Leven 2000; Carey et al. 2001). Velvet-fronted Nuthatches were first recorded in Hong Kong in 1989 and quickly became established at one forest site (Leven 1993; Kwok & Corlett 1999) but, despite isolated records elsewhere (Carey et al. 2001) have shown little further spread (Carey et al. 2002).

Baya Weavers have been recorded in Hong Kong since 1970 and breeding has occurred regularly at Mai Po Nature Reserve, in the northwest New Territories, since 1995 (Carey et al. 2001). The population appears to have remained stable at about 30 birds since then (Carey et al. 2002) and there is no evidence of any further spread (MR Leven pers. obs.). Common Mynas were first noted in Hong Kong in 1952 and a small population appears to have become established in farmland areas in the New Territories by the end of the 1950s, at which time flocks of up to 30 birds were noted occasionally (Herklots 1967).

There appear to have been no subsequent changes in numbers and this species remains localized (Carey et al. 2001). House Crows were first recorded in Hong Kong in 1974 (Chalmers 1986) but by 1998 there were only a total of 12 records of one or two individuals and this species was not considered to be established in Hong Kong by Carey et al. (2001). Numbers have increased since and a population of approximately 100 birds is now present in the urban area of Kowloon with a distribution centred around the container port and associated cargo handling facilities (PJ Leader pers. com.).

The second sub-group, of ten species, includes Red-whiskered Bulbul, seven babblers and laughingthrushes (Streak-breasted Scimitar-babbler, Rufous-capped Babbler, Chinese Babax, Greater Necklaced, Black-throated and White-browed Laughingthrushes and Red-billed Leiothrix), Vinous-throated Parrotbill and Yellow-cheeked Tit. Red-whiskered Bulbul is only tentatively included in this group as it appears to have reached Hong Kong in colonial times, but the point of origin and vector is uncertain. Swinhoe (1861) recorded this species in Guangzhou in adjacent Guangdong Province but not in Hong Kong, though it had reached Hong Kong by 1903 (Kershaw 1904). It is unclear whether Hong Kong was colonized from Guangdong Province and it is also unclear whether the Guangzhou population had itself been introduced by people. However, this species is almost entirely absent from forest in both Hong Kong and Guangdong Province (Lewthwaite 1996; Kwok & Corlett 1999, 2000) and, on this basis, it appears likely to be alien to the region.

The seven species of babblers and laughingthrushes in this category were first recorded in Hong Kong as follows: Black-throated Laughingthrush and Red-billed Leiothrix (pre 1913), Streak-breasted Scimitar-babbler (1949), Chinese Babax (1959), White-browed Laughingthrush (1961), Greater Necklaced Laughingthrush (1969) and Rufous-capped Babbler (1985) (Vaughan & Jones 1913; Herklots 1967; Chalmers 1986; Carey et al. 2001). These species, with the exceptions of Streak-breasted Scimitar-babbler and Rufous-capped Babbler, were treated as natural colonists by Chalmers (1986). Subsequently, Streak-breasted Scimitar-babblers were also considered to be of natural origin by Leader (1993). However, a review of the patterns of occurrence and spread of all seven species resulted in their being treated as derived from captive stock by Carey et al. (2001).

Streak-breasted Scimitar-babblers, Rufous-capped Babblers, and Greater Necklaced and Black-throated Laughingthrushes now have well-established and expanding populations in forest and shrubland (Leven 2000; Carey et al. 2001; Carey et al. 2002). Chinese Babax has only become established above 650 m elevation on Tai Mo Shan in the central New Territories, Hong Kong's highest mountain, where a small population appears to have persisted since at least the date of the first observation in 1959 (Carey et al. 2001). Red-billed Leiothrixes were first noted in Hong Kong prior to 1913 (Vaughan & Jones 1913) but it was not until the 1980s that they became widespread (again in shrubland and forest) (Chalmers 1986) and, after peaking in the mid-1990s (Carey et al. 2001), the population has since decreased (Carey et al. 2002). Unlike the other species in this group, White-browed Laughingthrushes do not occur in forest but are found in shrubland and farmland (Leven 2000). Numbers of this species apparently peaked in the late 1970s and have since declined (Carey et al. 2001).

Vinous-throated Parrotbills were first recorded in Hong Kong in 1960 and a population has become established at above 600 m elevation on Tai Mo Shan since 1980 (Carey et al. 2001). Whilst irregular records from elsewhere in Hong Kong were considered to relate to birds of captive origin (Chalmers 1986), the Tai Mo Shan population was thought to be derived from natural colonists by Leader (1993). However, a review of the pattern of records in Hong Kong and Guangdong Province led to this population being treated, once again, as derived from captive stock by Carey et al. (2001).

The first record of a Yellow-cheeked Tit in Hong Kong occurred in 1988 and breeding was first recorded in Tai Po Kau forest—Hong Kong's largest contiguous forest area—in 1989 (Chalmers 1990). A small population has persisted at this site but, despite occasional records from other forest localities as well as in shrubland and urban parks, no other populations have become established (Carey et al. 2001). This species was originally considered to have colonized Hong Kong naturally (Chalmers 1990), however Carey et al. (2001) considered that all records of this species in the territory were derived from birds of captive origin.

ECOLOGICAL IMPACTS OF INVASIVE BIRD SPECIES IN HONG KONG

The species listed in Table 1 are long-established

components of Hong Kong's avifauna. Seven of the nine species (all except for Black-collared and White-shouldered Starlings and Scaly-breasted Munia) are among Hong Kong's 20 most widespread breeding bird species (Carey et al. 2001). In contrast, of the 19 species in Table 2, only one, the relatively long-established Red-whiskered Bulbul, falls within this category. This bulbul is Hong Kong's second most widespread breeding bird, occurring in 72% of 1 km squares in the territory (Carey et al. 2001). Taken together, however, exotic species are now a substantial element of the breeding avifauna, comprising over 20% of the 141 species that were recorded breeding in Hong Kong during the mid 1990s (Carey et al. 2001).

The diversity and abundance of exotic bird species in Hong Kong suggests that they must be of some ecological significance, but there is little direct evidence of their ecological impact. The long-established species, which comprise all but one of the most widespread exotics, would be expected now to be in equilibrium with the native flora and fauna, so any impacts of their arrival would be impossible to detect. Furthermore, all of these species largely or entirely utilize anthropogenic habitats, so they interact only with other exotics and the most tolerant of native species.

Of the species that have invaded Hong Kong in historical times, both Yellow-crested Cockatoos and Rose-ringed Parakeets cause temporary damage to trees in city parks by feeding on growing shoots (Herklots 1967). The Yellow-crested Cockatoo also causes similar damage to native trees in secondary forest on Hong Kong Island and occasionally destroys whole crops of unripe fruits (T Corlett pers. obs.). These birds are not abundant enough for these impacts to be serious, but any future increase in parrot populations should be viewed with some concern. Perhaps more significantly, it has been suggested that these species may have been implicated in the disappearance of the native Great Barbet *Megalaima virens* from Hong Kong Island, presumably by competition for nesting holes (Carey et al. 2001). This can be excluded as an explanation in the case of Yellow-crested Cockatoo, as Great Barbets vanished from Hong Kong Island prior to the occurrence of the cockatoos, but the disappearance of the barbets did coincide with the period of peak abundance of the parakeets.

As noted above, the Red-whiskered Bulbul is the most widespread of the species that have invaded

Hong Kong in historical times. This bird has been considered a potential pest species elsewhere in the world where it has been introduced (Long 1981). In Hong Kong, it is one of the commonest species in urban parks (Lock 2000) and it is also abundant in farmland and shrubland, where it co-exists with and is outnumbered by the closely related Chinese Bulbul *Pycnonotus sinensis* (Leven 2000). However, it is rare in forest (Kwok & Corlett 1999, 2000) and there is no reason to suppose that it has had any impact on the numbers and distribution of any native species in Hong Kong in natural habitats. The Red-whiskered Bulbul is highly frugivorous and probably the third most important seed dispersal agent in Hong Kong (after *P. sinensis* and *Z. japonica*) in terms of numbers of seeds dispersed (Corlett 1998, 2002; MR Leven unpubl, S So unpubl.). Its impact on woody succession in open habitats is therefore likely to have been positive.

Both the Common Magpie, which is considered to have invaded during colonial times, and the Large-billed Crow, which arrived in the 1930s, are known as nest predators (Ali & Ripley 1986). However, both species are largely absent from wooded habitats (Kwok & Corlett 2000; Leven 2000), unlike the native Red-billed Magpie which appears to be at least as effective as a nest predator in Hong Kong (Herklots 1967; Viney 1995).

Although most of the species that have become established in forest habitats without human assistance are apparently generalist insectivore-frugivores, they also include: four predators on vertebrates, one a specialist on snakes (Crested Serpent Eagle); the only species occurring regularly in Hong Kong which is capable of making its own nest holes in trees (Great Barbet); and the most nectarivorous bird species now occurring in Hong Kong (Orange-bellied Leafbird and Fork-tailed Sunbird). These species must have had some impact on the recovery of Hong Kong's forest ecosystem and, while it is tempting to assume that as natural colonists from Southeast China their impacts have been benign, there is no firm evidence of this.

Potentially of greater concern are the suite of species that have been introduced into forest habitats in Hong Kong as a result of human actions (five species of babbler, three laughingthrushes, Yellow-cheeked Tit and Velvet-fronted Nuthatch). In all these species, populations have become established since the 1950s and the numbers and distribution of six species (Streak-breasted Scimitar-babbler, Rufous-

capped Babbler, Greater Necklaced Laughingthrush, Black-throated Laughingthrush, Silver-eared Mesia and Blue-winged Minla) are currently increasing (Carey et al. 2001; Carey et al. 2002). As far as is known, none of these species was released with the deliberate intention of establishing a wild population. More likely, their establishment in Hong Kong in recent years is a consequence of an increase in the area of suitable forest habitat co-incident with an upsurge in the bird trade from southern China and the increased popularity of releases of birds from temples (Melville & Lau 1994; Severinghaus 1999; Carey et al. 2001).

Most of these introduced species have native populations in Guangdong Province, and it seems likely that they were present in Hong Kong prior to deforestation. As a result, their establishment has generally been welcomed as contributing to the restoration of Hong Kong's avifauna and of bird-dependent ecological processes. The Greater Necklaced Laughingthrush, in particular, is now the largest-gaped avian frugivore in many areas of shrubland and secondary forest, capable of swallowing fruits that are too big for any other common bird species and thus restoring seed dispersal services for species that were un- or under-dispersed previously (Corlett 2002). This species also appears to have permitted natural colonization by the Red-winged Cuckoo, a brood parasite for which this species appears to be a primary host (Becking 1981; Carey et al. 2001).

However, relying on informal releases of traded birds as a means of reintroduction is risky at best. The source or sources of the released birds is usually unknown, but will rarely, if ever, be the nearest wild population to Hong Kong. At least one established sub-population of Greater Necklaced Laughingthrushes shows characters of a race from western China (rather than the race *G. p. picticollis*, which is present in Guangdong Province) (Carey et al. 2001) and there is some evidence that more than one race of Streak-breasted Scimitar-babbler may have been introduced (MR Leven pers. obs.). Even where there are no visible racial differences, birds captured in areas remote from Hong Kong are likely to be genetically distinct from the nearest populations and thus less suitable for reintroduction. It is also probable that some introduced populations have been established from very few released birds and will therefore be genetically impoverished. While these "informal reintroductions" have demonstrated the potential for ecological restoration in Hong Kong, they have also, presum-

ably, occupied the available niches for these species, making planned reintroductions of the appropriate races from the nearest available source population difficult or impossible.

The two species introduced to montane shrubland, Chinese Babax and Vinous-throated Parrotbill, are also considered by Carey et al. (2001) to have potentially been present in Hong Kong prior to deforestation. Populations of both species have persisted on one mountain in Hong Kong but appear to be restricted to habitat above 600 m, which is similar to their lower altitudinal limit in Guangdong Province (Lewthwaite 1996). As such, the ecological impact of their introduction is probably limited.

Three of the introduced forest species, Silver-eared Mesia, Blue-winged Minla and Velvet-fronted Nuthatch, do not occur in the wild in southeast China (Lewthwaite 1996; Carey et al. 2001). The ecological consequences of their introduction are unknown, though the Silver-eared Mesia may be competing directly with the congeneric Red-billed Leiothrix. The ability of these exotic species to establish in semi-natural forest communities presumably reflects the very impoverished nature of Hong Kong's forest avifauna, from which most of the expected babblers are missing. Their establishment may have pre-empted the reintroduction of species that were present before deforestation, although the Velvet-fronted Nuthatch occupies a niche with no obvious competitors in the present or past avifauna.

The Common Myna is a highly invasive species elsewhere in the world and has had significant impacts on native species, especially on islands (Storer 1931; Feare & Craig 1998; Yap & Sodhi 2004). In Hong Kong, a population has persisted for 50 years but there is no evidence that it has increased beyond the size that it reached within a few years of colonization. The reasons for the failure of Common Myna to prosper in Hong Kong are unclear. However, the largest group in recent years has occurred in the only area where (feral) water buffalo remain in Hong Kong (Carey et al. 2001) and it may be that elsewhere in Hong Kong it is largely excluded by Crested Myna, a species with which it overlaps naturally only in a limited area in southwest China (Cheng 1987).

Potentially the greatest ecological concern attaches to the recent increase in numbers of House Crows. Currently, the population is restricted to a limited geographical area and is wholly urban. At present, it is unlikely to be interacting with native wildlife to a significant extent and the known roosts are in large trees

in small city parks (P.J. Leader pers. com.), which are of limited importance for wildlife, though these parks are of considerable amenity value. However, the population is geographically close to the only egretty in the Hong Kong harbour area (Wong 2002). This is of concern in view of the House Crow's known adverse effects on ardeid colonies elsewhere in the world (Ryall 1992). Based on experience elsewhere, the population may already have reached a point where eradication would be very difficult (Ryall 2003).

Numerous other exotic species have become established in Hong Kong over recent decades but, in contrast to the birds, these are largely in lowland anthropogenic habitats (Dudgeon & Corlett 1994). The best-studied exotic group is the plants, which so far have not invaded upland shrubland and forest habitats (Ng & Corlett 2002). The same pattern seems to be true for other, less studied, groups, with a very few exceptions. The clearest analogy with the birds considered in this paper is Pallas's Squirrel (*Callosciurus erythraeus*), which became established in Hong Kong around 1970, from escaped or released pets (Dudgeon & Corlett 1994). Previously, there were no native squirrels in Hong Kong, presumably as a result of deforestation. Squirrels are now widespread in forest and shrubland on Hong Kong Island and in parts of the New Territories. Two different subspecies have become established as result of at least two separate introductions of squirrels from different parts of the species' range. The squirrels have increased pre-dispersal seed predation, as well as being responsible for bark stripping and bud damage. However, Hong Kong is within the natural range of *C. erythraeus*, so these impacts could be viewed as a restoration of natural ecological processes.

CONCLUSIONS

As a consequence of early deforestation of the Hong Kong region, the pattern of invasion by exotic bird species is very different from that which is currently being recorded elsewhere in tropical East Asia (Wells 1999; Yap & Sodhi 2004). With the exception of Red-whiskered Bulbuls, which appear to have colonized Hong Kong in the latter part of the nineteenth century, and perhaps House Crows which may be on the brink of a rapid population increase, Hong Kong has not been colonized in historical times by open country generalists or granivores that have rapidly become abundant in anthropogenic habitats. Rather, recent invaders of Hong Kong are forest species that

have been brought to Hong Kong for sale as cage-birds or for release from temples. The majority of species are babblers and laughingthrushes, which are insectivore-frugivores (Corlett 1998; Leven 2000). Rather than being opportunists with widespread distributions, these species are Indo-Himalayan in origin (Clements 2000) and the apparent source populations of most species are forests in southern China (Carey et al. 2001). Thus, entirely fortuitously, many of the species that have recently invaded Hong Kong are likely to have been present in Hong Kong's primeval forests.

This apparent paradox is explained when the probable origins of Hong Kong's widespread open country species are examined. Many of these species are wholly or largely restricted to anthropogenic habitats in Hong Kong that almost certainly had no equivalent in the territory before deforestation. The inescapable conclusion is that Hong Kong experienced a wave of colonization by adaptable open country bird species prior to the beginning of our historical records of bird distribution. The pattern of invasion of bird species in Hong Kong thus provides a possible model for the future evolution of bird communities elsewhere in the region.

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Southeast Asian invasive birds: ecology, impact and management

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Abstract Invasive birds can have serious impacts on native biodiversity, native ecosystems and humans. However, there is a dearth of literature on the status and effects of invasive birds in Southeast Asia. We review the current available information on the invasive bird species in Southeast Asia, first by discussing characteristics that likely make invasive bird species successful and second by reviewing the impacts of the invasive bird species on Southeast Asian economy and biodiversity. We end by discussing the strengths and weaknesses, as well as the applicability of different management options.

Key words Exotic birds, Invasions, Management, Tropics

The negative impact of invasive species on native biodiversity and ecosystems has been widely recognized for decades (Elton 1958; Lodge 1993a, b; Simberloff 1996). In addition, invasive species can be devastating for human economy (Pimental et al. 2000). Most long-distance introductions of non-native species to new areas are the direct or indirect results of human activities, and social and economic factors are often as critical as biological factors in the introduction of exotic species. Activities such as logging and grazing further enhance establishment of exotics by creating optimal habitat for colonization. Agriculture also facilitates species invasions when pests in agro-ecosystems are exposed to agricultural practices for many generations, resulting in selection for characteristics that make them persistent and noxious (Sakai et al. 2001). Southeast Asia is currently experiencing extensive development through urbanisation and deforestation (Wilson 1988; Myers 1992; Flint 1994). In light of these anthropogenic changes to the environment that can potentially precipitate future invasions of exotic species, it is important to examine the ecology, impact and management of invasive birds in Southeast Asia.

Invasive birds are defined as non-indigenous species that have spread from the point of introduc-

tion and become abundant (Kolar & Lodge 2001). Many of these species threaten local economies, human health and native biota (Kolar & Lodge 2001; McNeely 2001). In this paper, we focus on bird species that have invaded Southeast Asian countries, namely Indonesia, Malaysia, Singapore, Vietnam, Thailand, Cambodia, Laos, Burma (Myanmar) and the Philippines. A literature search using key words relevant to the topic was performed using the databases ISI Web of ScienceSM (1988–2003) and ScienceDirect[®] (1966–2003), as well as from books concerning this topic. We consider all non-native bird species that have established through either natural range expansion or deliberate release. We refer to the non-native bird species that have spread from the point of introduction and established populations as invasives or exotics. By referring to species accounts by Long (1981), Lever (1987) and Robson (2000), we identified 16 species, which had invaded and established in one or more of the abovementioned countries (Table 1). The small pool of information retrieved suggested a dearth of knowledge on the invasive species of Southeast Asia. This is in contrast to the situation in Australasia (Australia, New Zealand, New Guinea and surrounding islands), which has one of the best-documented and most completely analysed datasets available on biological invasions (Brook 2004).

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Table 1. Characteristics of Southeast Asian invasive bird species.

Species	Colonised Location	Mode of Colonization	Some Species Characteristics	Relationship with humans or other species of birds
Spotted Dove <i>Streptopelia chinensis</i>	Indonesia; Philippines	Unknown.	Inhabits open forest, secondary growth, wooded and cultivated country, parks, rivers, residential and urban areas; can occur in flocks; mainly sedentary; its diet includes seeds, grain, green shoots and food scraps; multi-brooded and probably breeds throughout the year; adaptable in choice of nest site; lays 2 eggs.	Potential crop pest.
Peaceful Dove <i>Geopelia striata</i>	Thailand; Borneo; Indonesia; Philippines; Laos.	Deliberate introduction by natives.	Common cage bird; inhabits dry forest, arid scrubland, open country, cities, villages, gardens, farms and cultivated areas; can occur in flocks; sedentary and nomadic; its diet includes seeds, grain (including cultivated grain), insects, small invertebrates and food scraps; lays 2 eggs; multi-brooded, probably breeding throughout the year.	Confiding and allows close approach by humans; well-adapted to exploit human-altered habitats.
Feral Pigeon <i>Columba livia</i>	Most of Southeast Asia (with possible exception of Vietnam).	Feral.	Inhabits cities, towns, villages, farms, cliffs; can occur in flocks; sedentary; its diet includes seeds, grain, green shoots, berries, earthworms, slugs, snails; multi-brooded and breeds most of the year; lays 2 eggs; feeds young cropmilk; breeds from young age of six months.	Strong commensal ties with humans; considered nuisance because of fouling of buildings and other structures and grain with its droppings; agricultural pest; useful as food, bioindicator and for study of avian biology.
Moustached Parakeet <i>Psittacula alexandri</i>	Borneo; Singapore.	Escapee from cage.	Inhabits secondary jungle, forest, woodlands near cultivation and mangroves; can occur in flocks; sedentary; its diet includes seeds, nuts, fruits, berries, nectar blossom and leaf buds; hole-nester; lays 3 to 4 eggs.	Potential rice crop pest.
Yellow-crested Cockatoo <i>Cacatua sulphurea</i>	Singapore.	Unknown.	Inhabits open woodlands, cultivated fields and forest edges; can occur in flocks; its diet includes seeds, nuts, berries, fruits; hole-nester; lays 2 to 3 eggs (in captivity).	
House Crow <i>Corvus splendens</i>	Malaysia; Singapore.	Released as a biological controller of pests; Natural expansion.	Inhabits plains, mangroves, villages, towns and cities; can occur in flocks; sedentary; its diet is omnivorous and includes insects, termites, locusts, grain, nectar, fruit, offal, carrion, eggs, and young birds; useful scavenger; lays 3 to 6 eggs; solitary or colonial nester; nests on variety of substrates; roosts communally in hundreds.	Potential crop pest; attacks small birds and eats their eggs; competes with native species and destroys their nests and eggs; communal roosts annoy residents.
Common Myna <i>Acridotheres tristis</i>	Vietnam; Malaysia; Singapore; Thailand.	Natural expansion; Introduction.	Inhabits primarily human habitation, also open country, forest edges, agricultural land, gardens, orchards, towns, cities and villages; can occur in flocks; roosts communally in large flocks; sedentary; its diet is omnivorous and includes fruits, grain, seeds, berries, insects, earthworms, flower nectar; multi-brooded; hole-nester; lays 3 to 6 eggs.	Possible crop pest; largely commensal with man; considered possible biological controller of insect pests, but at other times cause damage to orchard fruit and standing cereal crop but does not affect cultivated fruits much; may compete for nesting holes with native bird species

Table 1. (Continued)

Species	Colonised Location	Mode of Colonization	Some Species Characteristics	Relationship with humans or other species of birds
White-vented Myna <i>Acridotheres javanicus</i>	Singapore; Malaysia.	Escapee from cage; Natural expansion from Singapore.	Inhabits cities and cultivated areas; opportunistic and its diet is omnivorous including seeds, fruit (including cultivated fruit), nectar, insects, animal matter, human refuse; sedentary; can occur in flocks; hole-nester; adaptable in choice of nest site; roosts communally in hundreds; adaptable in choice of nest substrate; lays 2 to 5 eggs.	Tolerant of humans; disturbs human residents near communal roosts; faecal droppings foul buildings and cars.
Crested Myna <i>Acridotheres cristatellus</i>	Malaysia; Philippines.	Released as a biological controller of pests.	Common cage bird in native range; inhabits plains, cultivated areas, fields, open country, parklands, villages, suburban gardens, orchards; mainly found on the ground where it frequently feeds in grassland, often among cattle; can occur in flocks; sedentary; its diet includes insects, worms, slugs, snails, mussels, fruits, nuts, grains; multi-brooded; hole-nester; may sometimes nest colonially; lays 4 to 7 eggs; roosts communally, sometimes in hundreds.	Considered by some to be a crop pest.
Sooty-headed Bulbul <i>Pycnonotus aurigaster</i>	Sumatra.	Unknown.	Common cage bird; inhabits secondary growth, open forest, scrub, gardens, parks, roadsides; can occur in flocks; its diet includes insects, fruits, nuts; multi-brooded; lays 2 to 6 eggs.	Has both beneficial and harmful impacts on the agricultural and forestry industry.
Red-whiskered Bulbul <i>Pycnonotus jocosus</i>	Singapore.	Escapee from cage.	Common cage bird; inhabits forest edges, secondary growth, woodlands, cultivation, parklands, gardens, villages; can occur in loose flocks; roost communally; sedentary; its diet includes fruits, berries, seeds, flowers, nectar, insects, caterpillars, ants, seedlings; multi-brooded; lays 2 to 4 eggs.	Causes some damage to fruits and vegetable gardens in Thailand and other countries; but also destroys insects in other countries; has both beneficial and harmful impacts on agriculture.
White-crested Laughingthrush <i>Garrulax leucolophus</i>	Singapore.	Unknown.	Inhabits thickets, forest undergrowth, secondary growth, bamboo jungle, scrub country bordering cultivation; can occur in flocks; sedentary; insects, berries, seeds, small reptiles, nectar; multi-brooded; lays 2 to 6 eggs.	
Eurasian Tree Sparrow <i>Passer montanus</i>	Philippines; Indonesia; Malaysia.	Accidental.	Inhabits wooded regions, open fields, grasslands, parks, gardens, orchards, villages, towns; can occur in flocks; roosts communally; mainly sedentary in Asia; its diet includes seeds, rice and other grains, insects; multi-brooded; lays 4 to 8 eggs; often colonial nester; versatile in nest site selection.	Potential grain crop pest.
Red Avadavat <i>Amandava amandava</i>	Sumatra.	Escapee from cage.	Common cage bird; inhabits wet grasslands, reeds, secondary growth, scrub, gardens, villages, cultivation (especially rice fields); can occur in flocks; sedentary; its diet includes seeds, grains, insects; lays 4 to 10 eggs.	Potential rice crop pest.

Table 1. (Continued)

Species	Colonised Location	Mode of Colonization	Some Species Characteristics	Relationship with humans or other species of birds
Scaly-breasted Munia <i>Lonchura punctulata</i>	Singapore.	Escapee from cage.	Common cage bird; inhabits secondary growth, open and timbered grassland, cultivated areas, ricefields, gardens, villages; will also feed in rubbish dumps and on roadkills; can occur in flocks; roosts communally; sedentary and nomadic; its diet includes seeds, rice, berries, insects; multi-brooded; colonial nester; adaptable in choice of nest-site; lays 4 to 10 eggs.	Rice crop pest.
Java Sparrow <i>Padda oryzivora</i>	Vietnam; Burma (Myanmar); Thailand; Indonesia; Philippines.	Escapee from cage.	Common aviary bird; inhabits rice fields, villages, cities, mangroves, scrub; largely associated with humans; can occur in flocks; sedentary; its diet includes corn, seeds, cultivated grains, insects; colonial nester; lays 4 to 8 eggs.	Potential rice crop pest.

NB: The information in the table was compiled from the following sources: Pinowski & Kendeigh (1977); Long (1981); Hails (1985); Lever (1987); Kang et al. (1990); Dickinson et al. (1991); Kang (1992); Madge & Burns (1994); Johnston & Janiga (1995); Pell & Tidemann (1997); Restall (1997); Feare & Craig (1999); Robson (2000); Gibbs et al. (2001); Peh & Sodhi (2002).

SOME COMMON CHARACTERISTICS OF INVASIVE SPECIES

Life history and ecological attributes are important influences on introduction success, and an understanding of them can be useful in the development of management strategies for invasive bird populations and of predictive models for bird invasions, which can identify high-risk species that require more attention concerning their intentional introduction (Johnston & Janiga 1995; Cassey 2002). Specific characteristics can assist a species in establishing in a new area (Mayr 1965; Duncan et al. 2003). The invasive birds listed in Table 1 show some characteristics that individually or collectively enhance the survival and reproductive success of invasive bird species and thus may have helped in their colonization, establishment and spread. We discuss these characteristics with reference to Southeast Asian invasive bird examples.

All the identified invasive species show social behaviour, such as facultative colonial nesting, communal roosting, and congregation at food sources. The likely benefits of this social behaviour include enhancement of predator avoidance, foraging, reproductive and locomotive efficiency (Johnston & Janiga 1995). Among colonists in man-made habitats, granivores are conspicuously more successful than insectivores. For example, the Feral Pigeon *Columba livia*, Scaly-breasted Munia *Lonchura punctulata*, Spotted

Dove *Streptopelia chinensis*, Peaceful Dove *Geopelia striata* and Eurasian Tree Sparrow *Passer montanus* are largely granivorous. This suggests that seeds may be a more amply available food resource in areas modified by humans. The birds listed show flexibility in the use of nest-sites. The White-vented Myna *Acridotheres javanicus* and the Common Myna *A. tristis* for example, use a wide variety of nest holes such as holes in the trunk of trees, drainage holes in retaining walls, holes in buildings, bridges and crevices in other structures such as lamp-posts, air-conditioners, ventilators and disused vehicles (Kang et al. 1990). All the identified species show habitat flexibility, a character that has been shown to increase the likelihood of successful avian invasion (Cassey 2002). Most of them can be found in man-altered habitats, such as agricultural land, villages and towns, or other disturbed habitats such as secondary growth, scrub and wooded country. This is in contrast to the invasion pattern seen in Hong Kong, another part of tropical East Asia, where most of the recent invaders are forest species. These differences in colonized habitat have been attributed to differences in recent patterns of habitat change by humans in Southeast Asia and Hong Kong (Leven & Corlett 2004). Many of the Southeast Asian invasive species, such as the Crested Myna and the White-crested Laughingthrush, are multi-brooded and sedentary, resulting in high bird densities. Jones (1996) suggested that successful

invasive birds had high reproductive rates and maintained high flock densities. Some species such as the Feral Pigeon are capable of breeding throughout the year, partly because they rely on seeds as their major food source, which are available throughout the year. They can also breed successfully at an early age (Dorzhiev 1978; Johnston & Johnson 1990). Breeding at an early age and throughout the annual cycle may result in high reproductive rates and help these species to spread in colonized areas. Columbids such as the Feral Pigeon also feed their young on regurgitated crop milk (seeds mixed with secretions from the crop). This habit bypasses the routines of normal altricial birds of hunting for high-protein arthropods, whose availability may vary stochastically, to feed their young (Johnston & Janiga 1995).

Ricklefs (1969a, b) pointed out that hole-nests suffer less mortality, both in terms of individual and whole nest losses, than do open nests. The Eurasian Tree Sparrow, for example, is a hole-nester, and it likely experiences little predation pressure, in contrast with open-nesting birds. Hole-nesting species also do not experience stress due to severe micro-climatic changes (Dyer et al. 1977). Therefore, this habit may have assisted in the successful reproduction of some hole nesting species such as the Eurasian Tree Sparrow in newly colonized areas. Some species such as the Eurasian Tree Sparrow also possess a functional crop, which allows them to eat rapidly, minimising actual feeding time and thereby maximising the time available for searching for patchily distributed seed concentrations, and further allows an individual to take as much as possible from a localized food source before other individuals discover it (Wiens & Johnston 1977). The crop also allows birds to store large quantities of seeds temporarily for efficient transport to safer locations such as cover (Wiens & Johnston 1977). Hence, the presence of a crop may have allowed some invaders to compete better with the native species.

IMPACT OF INVASIVE BIRDS ON HUMANS

The establishment of invasive bird populations may affect the humans living there, since many of these species are found in human-altered habitats. This section outlines some known negative effects of invasive bird species recorded for Southeast Asian countries.

Where the Java Sparrow *Padda oryzivora* has been introduced in eastern Malaysia, it has been causing

damage, particularly on Labuan Island, since the late 1800s. It is said to cause serious damage to paddy *Oryza sativa* (Long 1981). According to Boosey (1958), it is a much-dreaded perennial curse in the rice fields of Southeast Asia, descending in hordes to devour the ripening grains. When the rice is ripening, it gathers in large flocks and obviously is capable of consuming considerable amounts, which naturally leads to its persecution. It would also feed on small fruits and possibly insects (Bernstein 1861). Like many species of munias, the Scaly-breasted Munia flocks to the paddy fields when the rice is ripening, feeding heavily from the laden panicles. In the Philippines, it causes damage to crops, principally rice (Long 1981). The Red-whiskered Bulbul *Pycnonotus jocosus* is reported to do a certain amount of damage in fruit and vegetable gardens in Thailand and is probably a pest throughout most of its range (Deignan 1945). Baker (1922) recorded damage to fruits such as raspberries *Rubus idaeus*, oranges *Citrus* spp. and plums *Prunus* spp. by this species. It is regarded as exhibiting much potential as a pest, particularly in fruit growing areas (Long 1981). According to Cheng (1963), the Red-whiskered Bulbul also destroys insects; it is considered both good and harmful.

In Singapore, there is much concern about the nocturnal roosting behaviour of House Crows *Corvus splendens*, and the accompanying fouling of gardens, pedestrian paths, buildings, and vehicles beneath or near roosts. Excessive noise from roosts, especially in the early morning hours, has also caused annoyance. A public perception also exists that the House Crow may spread pathogens to humans. The accumulation of their faecal droppings is thus perceived as a health hazard (Peh & Sodhi 2002), although Cooper (1996) has found no evidence that the House Crow plays a role in pathogen dissemination. It is a useful scavenger and probably eats many injurious insects, but also attacks small birds and eats their eggs. According to Fitzwater (1967), it flies in and out of houses without restraint and pilfers anything edible.

In Southern Asia, the Common Myna is not generally considered a pest. It is largely a commensal of man and is frequently abundant around towns where it roosts communally. It feeds on fruits, berries and insects, but does not appear to affect cultivated fruits much (Long 1981). According to Sengupta (1968) and Ali & Ripley (1968–74), the species is a friend of the farmer doing immense good by eating many insect pests, but Ali & Ripley (1968–74) also state that

they often cause damage to orchard fruits and standing cereal crops. Because of their fruit-eating habits, the species is regarded by many as being a potential pest in areas where it has been introduced (Long 1981). Like the House Crow, the White-vented Myna and the Common Myna are considered pests in Singapore primarily because of their habit of roosting communally at night, often close to humans, where they disturb and irritate the residents with their noise and faecal droppings (Hails 1985).

The Feral Pigeon has become a nuisance in most of the larger cities in the world because of their fouling of buildings and statues with droppings. Few large cities and towns lack Feral Pigeons. It is also generally regarded as a potential health hazard to humans in urban environments (Long 1981). Pigeon droppings deface and accelerate deterioration of buildings, statues and automobiles, render fire escapes hazardous, sometimes land on unwary pedestrians, and produce objectionable odours especially when deposited in ceilings and on sills. There appears to be reasonable evidence that it provides a reservoir for ornithosis and plays some part in the transmission of such diseases as encephalitis and histoplasmosis (Shuyler 1963; Morris 1969). It is a common contaminator of grain destined for human consumption. Its nests can clog drainpipes. It is a granivorous bird and is a candidate for being a pest on human row-crops (e.g. wheat *Triticum aestivum*, barley *Hordeum* spp., maize *Zea mays*, milo *Sorghum bicolor* and peas *Pisum* spp.; Long 1981).

IMPACT OF INVASIVE BIRDS ON NATIVE BIRDS

The avifauna of Southeast Asia is currently threatened by habitat loss (Ehrlich & Ehrlich 1981; Myers 1979, 1992; Brook et al. 2003a). The presence of invasive birds could compound the survival pressures on the avifauna through predation, disturbance or competition for resources. This section considers the known and potential detrimental effects of invasive birds on native birds in Southeast Asia.

The Common Myna nests in tree hollows and may compete for these resources with native hollow-nesting species (Pell & Tidemann 1997). Huong and Sodhi (1997) postulated that one of the factors in the decline of the hole-nesting Oriental Magpie Robin *Copsychus saularis* in Singapore might be the spread of the mynas there. The nesting of the Common Myna on the same trees was also known to disturb

the nesting of the threatened Seychelles Magpie Robin *Copsychus schellareum* on Fregate Island in the Seychelles. These nest disturbances had an adverse effect on the breeding success of the robins (Komdeur 1996).

In Kenya, the House Crow was observed to raid the nests of ploceid weavers and other small bird species (Ryall 1992); hence it might be possible that the House Crow in Southeast Asia could pose a similar threat (for instance to White-vented Mynas; Kang 1989). Available evidence shows that where the Feral Pigeon has been abundant, the feral and wild forms (i.e. the Rock Pigeon) interbreed, and the wild pigeon is genetically consumed by the Feral Pigeon eventually. Johnston and Janiga (1995) anticipated that the number of Feral Pigeon colonies and individuals would increase, perhaps in some proportion to the increasing human population. Feral Pigeon increases might allow it to occupy a greater distributional range, which could promote contact with the wild Rock Pigeon in regions where it was formerly isolated. Johnston and Janiga (1995) hypothesize that such contacts will be a challenge to the continued existence of the primordial, because the Feral Pigeon has both survival and reproductive advantages relative to the wild Rock Pigeon.

MANAGEMENT OF INVASIVE BIRDS

Some of the invasive species listed are crop pests, while other species are undesirable because of their communal roosting behaviour or fouling of buildings and other property. Yet others have a potential for competing with native birds. The possibility of a need for the control and management of these birds may arise with the establishment of populations in pest proportions now or in the future. It is timely therefore, to discuss the possible methods of controlling bird populations and a few studies of habitat modification as feasible long-term control programmes in Southeast Asia and beyond.

1) Direct control of bird populations

Direct methods to reduce bird populations (e.g. killing and scaring) are not effective in the long term. A common reason is that an equilibrium in the number of birds is reached when control mortality is balanced by recruitment and juveniles, either by reproduction or by immigration of juveniles from other populations, taking the places of those removed by the control programme (Murton et al. 1972; Martin &

Martin 1982; Haag-Wackernagel 1993b). Further, the impacts of some methods (e.g. poisons, baits and explosives) on the ecosystem are not often adequately assessed in the control programmes (Dyer & Ward 1977).

Use of guns is common in rural environments, but not always feasible in cities, which is why urban control killing is done after having trapped or netted the birds. Trapping and netting are expensive, hands-on activities. Chemical products that either kill or stupefy the birds are likewise fractionally effective in most populations, being dose-dependent and dependent on the birds contacting toxic perches or feeding on toxic or stupefying baits. Detailed knowledge of the birds' biology is critical when using chemicals. Some repellents are toxic in excess and may kill birds that were intended to be merely stupefied. Toxic chemicals may not kill immediately, but incapacitate the birds for some time prior to death. Dead or dying birds and the toxic substances themselves are threats to the public health when children and household pets contact them (Johnston & Janiga 1995). The dying birds can also be a public relations problem for the wildlife managers (Weber 1979). Further, effects of reduction or elimination of the pest on the community of animals, such as the replacement of the target by another (and possibly worse) pest species should be considered (Dyer & Ward 1977).

2) Sterilization of birds

Other methods such as the sterilization of birds have been tried. Chemosterilants have been reported in birds such as starlings *Sturnus* spp. The problems with field use of chemicals lie in guaranteeing the action of the chemical, in the delivery of the material to the wild population and in the lack of species-specificity (Dyer & Ward 1977).

3) Scaring and bioacoustic techniques

Use of sounds (e.g. recorded distress calls, periodic explosions from acetylene cannons) and scarecrow dummies (e.g. plastic owls, snakes) are known to be effective in sending the Feral Pigeon and White-vented and Common Mynas elsewhere for short periods. However, birds habituate to such stimuli within a few days, and these techniques prove unsatisfactory ultimately (Hails 1985; Johnston & Janiga 1995).

4) Habitat Modification

Habitat manipulation has long been espoused as the proper way to manage wildlife species (Leopold

1939). Comprehensive information about the entire biology of birds (e.g. the feeding, nesting, breeding, roosting requirements and behaviour) is required for an effective habitat control programme (Johnston & Janiga 1995). The type of information required would depend on the nature of the disturbance caused by the invasive species. Habitat modification can take many forms, such as exclusion (e.g. blocking entrances to holes to prevent roosting or nesting, and installing netting to protect high-value crops), agricultural and horticultural methods (e.g. removing roost sites and planting bird resistant varieties of crops) and food removal (e.g. restricted feeding) (Fitzwater 1994; Johnston & Janiga 1995). Below we examine a few such studies aimed at developing appropriate pest bird control programmes employing habitat modification in Southeast Asia and elsewhere.

Control of House Crow populations: The global range of the House Crow has increased in the past 100 years, an expansion that either happened naturally or through deliberate release by humans (Ryall 1994). The House Crow is now established in many urban areas throughout Asia, where it roosts communally in large numbers (e.g. >20,000 birds; Siew et al. 1980). In Singapore, the House Crow population is estimated to be 130,000 birds (Brook et al. 2003b). Urban managers have faced great public concern over the nocturnal roosts of these birds (Peh & Sodhi 2002). Since 1973, the sole management measure carried out by the government of Singapore to control urban House Crow roosts has been periodic shooting at known roost sites to disperse roosting birds (Peh & Sodhi 2002). However, this management technique has proven ineffective in achieving long-term control. In a recent study by Peh & Sodhi (2002), it was found that the House Crow preferred roosting in tall, old trees such as *Pterocarpus indicus* with large dense crowns surrounded by tall buildings and located in areas of much human activity. Their study recommended the following habitat modification measures to discourage the crows from roosting in affected areas: (a) avoid planting well-spaced tall trees (18m tall) in urban area; (b) making existing roost sites less attractive (e.g. by tree pruning); and (c) establishing alternative roost sites. A study of the nest site selection of the House Crow in Singapore by Soh et al. (2002) found that it preferred nesting in *Peltophorum pterocarpum*, in trees with greater crown volume and diameter at breast height, in urban open habitats, with higher disturbance, and nearer to bin centres and food centres. They recommended the fol-

lowing habitat modification measures to discourage crows from nesting in affected areas: (a) minor changes to the design of existing bin centres (i.e. food source) to restrict access by crows; (b) planting alternative, less suitable tree species; and (c) regular pruning of trees with large and dense crowns. Brook et al. (2003b) argued that if applied simultaneously, both population control and habitat management might work effectively for the long-term control of House Crows in Singapore.

Control of Common and White-vented Mynas: These two species of mynas are well established and common in Singapore, where their populations are estimated to exceed 100,000 birds and 25,000 birds, respectively (Lim et al. 2003). They are considered pests in Singapore primarily because of their communal nocturnal roosts, which frequently occur in residential areas, where their noise and faecal droppings disturb neighbouring residents. This has led to calls for management, and to attempts by authorities in Singapore to remove the birds by scaring, poisoning, and thinning or removing the trees (Hails 1985; Kang et al. 1990). These measures were partially effective short-term solutions to the problem, probably because they were not integrated with serious efforts by the authorities to provide alternative roosting sites for the mynas in less humanly populated areas (Kang et al. 1990). Schmidt & Johnson (1984) proposed that the difficulties of roost dispersal might be reduced if stress was imposed on the birds by removing sources of food, water or shelter from the vicinity of the roost. Kang et al. (1990) argued that this strategy would be unsuccessful with the mynas because they had a highly diverse diet and choice of nesting sites, and they could range over a large area (e.g. 308.0 ha [Kang 1989] and 14.0 ha [Yap 2003]). Ecological studies have been carried out on mynas in Singapore with the aim of formulating habitat modification programmes to discourage mynas from roosting in affected areas. These studies found that mynas preferred to roost in tall, old trees with dense canopies, such as *Pterocarpus indicus* and *Eugenia grandis*, in urban areas sheltered from winds by nearby buildings or embankments, situated closer to food centres (i.e. open-air eateries) and surrounded by more vegetation than random non-roost trees (Hails 1985; Kang & Yeo 1993; Yap et al. 2002). Their studies recommended these management strategies: (a) roosts should be discouraged from forming in undesirable areas through a combination of bioacoustic and habitat modification control measures such as thinning of

canopies; (b) attractive alternative sites should be created in other areas (such as roadside verges or roundabouts situated away from residential areas) in numbers that kept pace with the myna population; (c) refuse should be stringently controlled at food centres; (d) planting of mono-specific rows of tall trees with dense canopies such as *Pterocarpus indicus* and *Eugenia grandis* in urban areas, especially near to food centres should be avoided, and trees with flattened, less dense canopies, or with leaves that close at night, such as *Samanea samanea* should be planted instead; and e) all these measures should be adopted on a long-term basis for effective control of myna roosts. Hails (1985) also recommended that roosts should not be disturbed unless they posed a serious nuisance, because of the costs and logistics involved in roost dispersal, and that public education be carried out at the same time.

Control of pigeon populations: A possible method of control of Feral Pigeon populations using modification of habitats would involve the elimination of food sources (including deliberate feeding of pigeons by people), and the cleanup of food waste and spillage. The control of food supply was the basis for a successful control programme of a Feral Pigeon population in Basel, Switzerland (Haag-Wackernagel 1993a). Prior experience in Basel showed that the population of Feral Pigeons was about 20,000 individuals, which numbers had been maintained in the face of the inadequate trapping and shooting of 100,014 birds in the period 1961 to 1985 (Haag-Wackernagel 1993b). The new programme envisioned population reduction, not elimination, by means of highly restricted feeding of just a few birds. A loft was created and the birds were fed nearby in a public place. A bird-keeper maintained the loft and took eggs and young when the population exceeded a certain predetermined number. The programme included public education on the advantages of population control, and the public advantages of having healthy, unstressed birds.

CONCLUSION

There are 16 established invasive bird species in Southeast Asia. These species may have some negative impacts on the native biodiversity and human economy. However, we need more research to assess the impacts of these species precisely. Control of invasive bird species in Southeast Asia is possible, but it requires a multi-pronged approach including both

population and habitat management.

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ORIGINAL ARTICLE

Are Carrion Crows that congregate in spring roosts juveniles or adults?

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Abstract Carrion Crows *Corvus corone* often establish spring roosts even during the breeding season. To examine whether the individuals roosting in spring are juveniles with immature reproductive organs, we compared the body size, sexual organs, and plumage of 150 roosting and 35 breeding individuals collected in the Joetsu region, Niigata, Japan, between 20 April and 9 May 1992. In both sexes, roosting individuals had significantly lighter bodies, and shorter wings and tails than breeding individuals. Roosting males had significantly lighter and shorter testes, and a lower testes/body percentage than breeding males. All 15 breeding males and 17 of 70 roosting males (24.3%) had mature testes, while 53 of 70 roosting males (75.7%) had immature testes. Roosting females had significantly lighter ovaries and a lower ovary/body percentage than breeding females. All 20 breeding females and 19 of 80 roosting females (23.8%) had long, enlarged oviducts, while 61 roosting females (76.2%) had undeveloped oviducts. Based on plumage characteristics, we estimated that 112 of the 150 roosting crows (74.7%) were juveniles. The reproductive organs of 108 of the 112 juveniles (96.4%) and 6 of 38 adults (15.8%) were immature. These results suggest that the spring roost consisted mainly of juveniles with immature reproductive organs. Thirty-six roosting individuals had mature reproductive organs. We considered them to be either territorial adults that had attempted to breed near the roost but failed, or sexually mature non-territorial males.

Key words Age, Carrion Crow, Reproductive organs, Roosting individual, Spring roost

Carrion Crows *Corvus corone* establish large roosts from autumn to winter, while they often form small roosts in spring, even during the breeding season (Kurata & Higuchi 1972; Koshio et al. 1996; Nakamura 2003; Yoshida 2003). Breeding adults remain on their territories and sleep near the nest at night (Haneda & Iida 1966; Nakamura 1998; Yoshida 2003). Therefore, many authors assume that individuals congregating in spring roosts are sexually immature juvenile birds (e.g. Goodwin 1986). However, there is no direct evidence for this.

The best way to identify roosting birds as sexually immature birds is to collect roosting birds and examine their internal reproductive organs. Carrion Crows were shot as pest birds in the spring of 1992 in the

Joetsu region, Niigata, Japan and we obtained a total of 185 individuals. Carrion Crows can be aged by their plumage (Busse 1984). Our aim was to determine whether the individuals roosting in spring are juveniles with immature reproductive organs, based on the development of their reproductive organs, and examine the relationship between age and the development of reproductive organs.

STUDY AREA AND METHODS

Crows were shot around the campus of Joetsu University of Education (37°08'N, 138°14'E, 15–25 m elevation), Joetsu City, Niigata, and in an 8×4-km area (37°07'N, 138°19'E, 15–20 m elevation) at Sanwa-mura, Nakakubiki-gun, Niigata, between 20 April and 9 May 1992. The latter area was about 22 km from the university. A forest on the campus of the university has been used as a roost mainly by

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Carrión Crows throughout the season for at least 25 years (Tanaka 1989; S. Murayama unpubl.). Roosting individuals (those that congregate in the spring roost in the evening) were shot around the university and we obtained 150 specimens. To compare the body size, plumage characteristics, and reproductive organ development between roosting and breeding individuals, 35 breeding individuals were shot during the nestling period in the study area at Sanwa-mura. The shooting period corresponded to the nestling period in our study population. Members of the Japanese Hunting Association had authority to shoot the crows and we went along with them to collect specimens.

For each specimen, four measurements were recorded as body size: (1) body mass, measured to the nearest 0.1 g with an electronic balance; (2) wing length, the maximum distance from the carpal joint to the tip of the longest primary in the flattened and straightened right wing; (3) tail length; and (4) tarsus length. All linear measurements were made to the nearest 0.1 mm with vernier calipers.

Age determination using plumage characteristics followed Busse (1984). Juveniles have dark brown greater and median coverts, and the tips of the tail wing are worn and cut off conically, while adults have metallic black greater and median coverts, and the tips of the tail wing are not worn and are cut off perpendicularly.

Within two hours of collecting each specimen, we removed the entire reproductive tract and determined the sex. In males, each testis was removed and weighed to the nearest 0.01 g on an electronic balance. We measured the testes length (major and minor axes) with vernier calipers to the nearest 0.1 mm. The testes length (major axes) of Carrión Crows from central Hokkaido was found to increase from March to May (Tamada & Fujimaki 1993), however, in our study area no such increase was observed during the shorter period from 20 April to 9 May (roosting males, $F_{1,68}=1.85$, $P=0.18$; breeding males, $F_{1,13}=3.90$, $P=0.70$). Thus, the data were pooled for 20 days.

After we measured testes size, the testes were fixed in Bouin's solution for 48 h and preserved in 70% ethanol. The testes were prepared for routine histology: 8- μ m-thick paraffin sections were stained with Mayer's hematoxylin-eosin and examined under a light microscope. The testes of all avian species undergo marked changes during the development of spermatogenesis. Immature testes are characterized by thin seminiferous tubules, which are largely full of

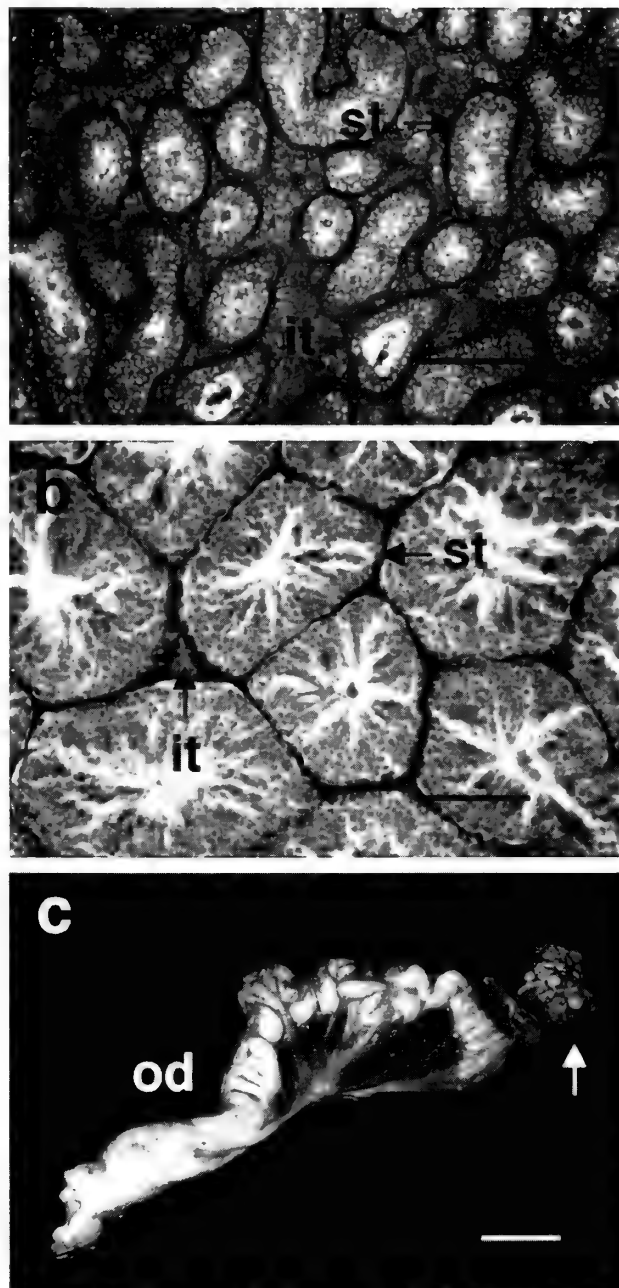


Fig. 1. Microscopic (a and b) and macroscopic (c) features of the gonads from male (a and b) and female (c) Carrión Crows. a: immature testis, characterized by thin seminiferous tubules (st) that are largely occupied by spermatogonia and by well-developed interstitial tissue (it). Scale indicates 50 μ m. b: maturing or mature testis showing active spermatogenesis in thick seminiferous tubules (st) and compressed interstitial tissue (it) between adjacent tubules. Scale indicates 50 μ m. c: a long, enlarged oviduct (od); arrow shows ovary. Scale indicates 30 mm.

Table 1. Comparison of body and testes size of roosting and breeding males. Figures are means \pm SD.

	Roosting individual	Breeding individual	t	P
N	70	15		
Body mass (g)	631.1 \pm 49.2	680.0 \pm 50.7	3.47	<0.001
Wing length (mm)	32.8 \pm 1.4	34.8 \pm 0.8	5.47	<0.0001
Tail length (mm)	19.8 \pm 2.7	21.5 \pm 0.7	2.41	<0.05
Tarsus length (mm)	6.3 \pm 0.3	6.4 \pm 0.3	1.66	=0.101
Testes mass ¹ (g)	0.70 \pm 0.81	1.75 \pm 0.75	4.64	<0.0001
Testis length ² (mm)	1.03 \pm 0.45	1.56 \pm 0.27	4.36	<0.0001
Testes/body ³ (%)	0.11 \pm 0.12	0.26 \pm 0.11	4.41	<0.0001

¹ Combined mass of both testes.

² Major axis of the larger testis.

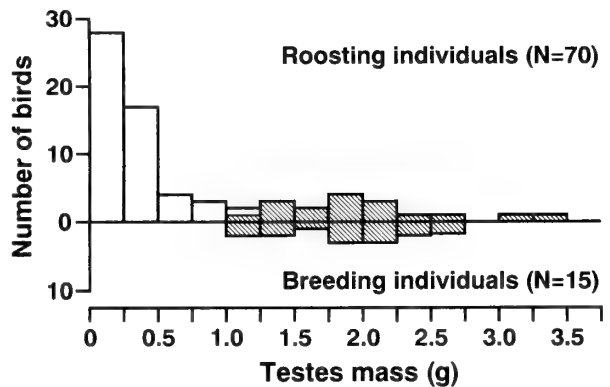
³ Combined mass of both testes as a percentage of body mass.

spermatogonia, and by well-developed interstitial tissue, while mature testes show active spermatogenesis, the seminiferous tubules have expanded enormously, and the interstitial tissue between adjacent tubules is greatly compressed (Lofts & Murton 1973). Based on the condition of the seminiferous tubules and interstitial tissues, we distinguished immature (Fig. 1a) and mature (Fig. 1b) testes. In females, the ovary was removed and weighed to the nearest 0.01 g on an electronic balance. Breeding females, particularly females that have laid eggs, have long, enlarged oviducts, but the oviducts become thinner during the non-breeding season (Gilbert 1979). We regarded long, and enlarged oviducts (Fig. 1c) as developed oviducts.

RESULTS

1) Males

Roosting males had significantly lighter bodies, shorter wings and tails than breeding males; while tarsus length was marginally, but not significantly shorter in roosting males (Table 1). Roosting males had significantly lighter and shorter testes, and a lower testes/body percentage than breeding males. However, overlap in these values was evident (Table 1). The frequency distribution of testes mass also showed considerable overlap (Fig. 2). All 15 breeding males and 17 of 70 roosting males (24.3%) had mature testes, while the remaining 53 roosting males (75.7%) had immature testes (Fig. 2). Based on age determination using plumage characteristics, all 15 breeding males and 23 of 70 roosting males (32.9%) were adults. The testes of 47 juveniles were immature. Of 23 adult males, 17 males had mature testes,


Fig. 2. Frequency distribution of testes mass (combined mass of both testes). Hatched bars are males with mature testes.

but six had immature testes.

2) Females

Roosting females had significantly lighter bodies, shorter wings and tails than breeding females, while tarsus length was marginally, but not significantly shorter in roosting females (Table 2). Roosting females had significantly lighter ovaries, and a lower ovary/body percentage than breeding females, although the values overlapped (Table 2). The frequency distribution of ovary mass showed considerable overlap between breeding and roosting females (Fig. 3). All 20 breeding females and 19 of 80 roosting females (23.8%) had long, enlarged oviducts, while 61 roosting females (76.2%) had undeveloped oviducts (Fig. 3). All 20 breeding females and 15 of 80 roosting females (18.8%) were identified as adults using plumage characteristics. All 15 adults had developed oviducts. Of 65 juvenile females, 61 had

Table 2. Comparison of body and ovary size of roosting and breeding females. Figures are means \pm SD.

	Roosting individual	Breeding individual	t	P
N	80	20		
Body mass (g)	537.9 \pm 43.0	602.6 \pm 39.7	6.10	<0.0001
Wing length (mm)	31.3 \pm 1.4	32.7 \pm 0.7	4.46	<0.0001
Tail length (mm)	19.1 \pm 1.9	20.3 \pm 0.6	2.82	<0.01
Tarsus length (mm)	6.0 \pm 0.2	6.1 \pm 0.2	1.81	=0.073
Ovary mass (g)	0.17 \pm 0.12	0.36 \pm 0.21	5.32	<0.0001
Ovary/body ¹ (%)	0.03 \pm 0.02	0.06 \pm 0.03	4.61	<0.0001

¹ Mass of ovary as a percentage of body mass.

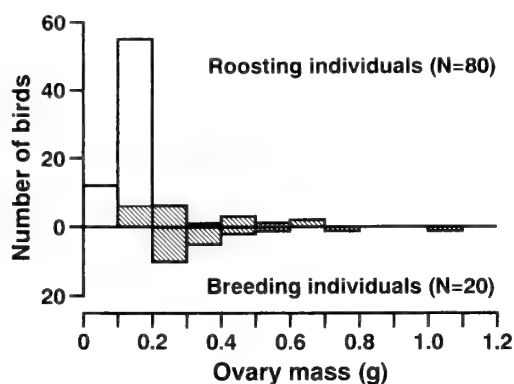


Fig. 3. Frequency distribution of ovary mass. Hatched bars are females with developed oviducts.

undeveloped oviducts, while four had developed oviducts.

DISCUSSION

It is clear that 114 of 150 roosting crows (76.0%) were non-breeders because they had immature reproductive organs. Based on plumage characteristics, we considered 112 of the 150 roosting crows (74.7%) to be juveniles. The reproductive organs of 108 of the 112 juveniles (96.4%) were immature. These results suggest that the spring roost was composed mainly of juveniles with immature reproductive organs. However, six roosting males estimated as adults had immature testes. Four roosting females had developed oviducts but were considered juveniles. Thus, plumage characteristics are not always consistent with sexual organ development.

Breeding adults likely roost near their nests to protect eggs and nestlings from predators. However, 17 males and 19 females with mature reproductive organs assembled in the spring roost. There are three possible explanations for this. First, individuals that

bred near the spring roost assembled in the roost. Kurata and Higuchi (1972) observed that some breeding adults assembled in a spring roost that was 4 km from their nests. Second, individuals that failed in breeding assembled in the spring roost because they did not need to protect eggs and nestlings. The Carrion Crow has two distinct social types: territorial pairs, and flocks of non-territorial individuals (Yoshida 2003). Pairs breed in territories (Nakamura 1998; Yoshida 2003), thus, sexually mature individuals that bred near the spring roost and failed in breeding must have had territories. Third, non-territorial adults assembled in the spring roost. Yoshida (2003) found that non-territorial individuals live in flocks until they can acquire a breeding territory, and the flock is composed of juveniles and individuals over two years old. Only rarely are females with developed oviducts non-territorial. Therefore, the individuals congregating in the spring roost would be sexually mature non-territorial males.

We concluded that spring roosts were composed mainly of non-territorial juveniles with immature reproductive organs and some sexually mature territorial adults that had attempted to breed near the roost but failed, or sexually mature non-territorial males.

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ORIGINAL ARTICLE

Habitat use and foraging behavior of male Black-and-white Warblers (*Mniotilta varia*) in forest fragments and in a contiguous boreal forest

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Abstract We examined habitat use and foraging behavior of male Black-and-white Warblers (*Mniotilta varia*) in fragments (2–140 ha) of mature forest dominated by trembling aspen (*Populus tremuloides*) and a similar contiguous forest (>1000 ha) in central Alberta, Canada. Vegetation structure and composition differed significantly between occupied and unoccupied fragments, and between plots within and outside territories in occupied fragments. Territories in fragments were characterized by a high abundance of willow (*Salix* spp.), which was the primary foraging site for males in this habitat. Territories in contiguous forest differed significantly in vegetation structure from territories in fragments, and were characterized by a high abundance of trembling aspen trees, which served as the primary forest foraging site. The use of foraging substrates and foraging methods did not differ between individuals in fragments versus contiguous forest. In the boreal mixedwood ecoregion, the Black-and-white Warbler appears flexible in its habitat use.

Key words Canada, Disturbance, Neotropical migrants, Vegetation, Wood warbler

In the last two decades, the proposition that fragmentation of forest habitat negatively affects songbird communities in temperate and tropical regions has become widely accepted by avian ecologists and conservationists. Some bird species will not occupy fragments (Schmiegelow et al. 1997), whereas in others, males establishing territories in fragments may not attract mates (Villard et al. 1993), or pairs nesting in fragments experience low reproductive success (Hinsley et al. 1999). The inferiority of fragments as nesting sites has often been linked to “negative edge effects” that create habitats that differ from contiguous forest in vegetative structure, production of food organisms, or risk from predation or brood parasitism (Hoover et al. 1995; Bayne & Hobson 1997; Burke & Nol 1998; Smith et al. 2000; Zanette et al. 2000).

Surprisingly few studies (e.g. Nour et al. 1997; Fleming et al. 1999; Miller & Cale 2000) have actually compared the behavior of birds in fragments versus contiguous forest, either in terms of habitat selection or foraging, to understand the possible reasons behind the apparent failure of fragments to offer suitable habitat or compensatory responses of birds inhabiting fragments.

The Black-and-white Warbler (*Mniotilta varia*) is a monogamous, ground-nesting species (Peck & James 1983; Ehrlich et al. 1988; Kricher 1995) that breeds in Nearctic forests but winters mostly in the Neotropics (O'Connor 1992). It is the only wood warbler species (Embrizidae: Parulinae) that frequently feeds on arthropods found on bark (Morse 1989). The Black-and-white Warbler is considered to be “area-sensitive” because in parts of its breeding range it does not occur in small forest patches (e.g. <10 ha in area; Villard et al. 1995) and tends to occupy forest-interior (>100 m inward from forest edge; Askins et al. 1987; Freemark & Collins 1992; Morneau et al. 1999). It has become locally extinct (Litwin & Smith 1992; Terborgh 1992) or shown long-term population declines (Sauer et al. 1996) in some areas, suggesting

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that it may be vulnerable to changing patterns of land use. However, the Black-and-white Warbler does display some degree of flexibility in habitat use as the species breeds in forests of different vegetation composition and ages across its range (Kricher 1995; Schieck et al. 1995; Dettmers et al. 2002).

We determined habitat use and foraging behavior of male Black-and-white Warblers in forest fragments and in a contiguous forest tract in the aspen-dominated boreal mixedwood forest of central Alberta near the northwestern edge of the species' range. Knowledge is slowly growing concerning the ecology of this species and other passerines in the western boreal forest, but populations certainly face rapidly changing conditions due to expansion of forestry, agriculture, and the energy sector (Schneider et al. 1999; Hobson & Schieck 1999; Hobson & Bayne 2000; Sykes & Hannon 2001).

The objective of our study was to examine to what degree songbirds occupying forest fragments display behavioral flexibility while documenting the specific habitat requirements and responses of male Black-and-white Warblers in the threatened boreal mixedwood forest. To do so, we addressed the following questions: (1) Within forest fragments, do Black-and-white Warblers establish territories in areas with particular habitat characteristics? (2) Do territories of the Black-and-white Warbler in forest fragments differ in their habitat characteristics from territories in contiguous forest? and (3) Do foraging patterns of male Black-and-white Warblers differ between forest fragments and contiguous forest? Based on continental and regional patterns for the species, we did not expect the Black-and-white Warbler to be a true habitat generalist, however, we did expect some flexibility in the species' behavior.

METHODS

The study was conducted around Meanook Biological Research Station (54°37'N, 113°20'W) near Athabasca, Alberta, Canada. Today, approximately 30% of the landscape is covered by forest dominated by trembling aspen, balsam poplar, willow, alder, white birch, and white spruce (scientific names of trees and shrubs in Table 1). In the past 50 years, the remaining area has been gradually cleared and converted to pasture or crop land. We selected eight forest fragments, dominated by mature (>80 yr old) trembling aspen, that ranged from 2 to 140 ha in area (2, 4, 6, 9, 32, 50, 113, and 140 ha; areas were calcu-

lated from 1:30,000 aerial photographs using a Placon® digital planimeter). We defined a forest fragment as a wooded area separated from other wooded areas by ≥ 30 m and/or connected to another wooded areas by a hedge/fencerow <10 m wide (cf., Villard et al. 1995). All forest fragments were located within a 9 km² area and excluded patches open to cattle grazing. For comparison with forest fragments, a 30-ha plot was established in a contiguous forest at Narrow Lake, about 13 km from the nearest fragment. This area was >1000 ha, dominated by mature trembling aspen trees, and known to contain Black-and-white Warblers. It should be noted that throughout this study sample sizes are relatively small, simply because the Black-and-white Warbler is generally uncommon. The species does not occur at high densities anywhere within its breeding range (mean=0.27 territories/ha [range=0.03–0.61]; data from 1993 Breeding Bird Census published in the Journal of Field Ornithology 1994 [supplement]). The study population, at the periphery of the species' range, displayed low densities (0.02–0.18 territories/ha; based on occurrences of individuals in occupied fragments and the contiguous forest plot).

1) Bird locations

All areas (fragments and contiguous forest) were flagged into 100×100 m grids. Grids were surveyed between early May and the end of June three times in 1993 (fragments only) and twice in 1994 (fragments and contiguous forest) to locate male Black-and-white Warblers. Locations of male Black-and-white Warblers were plotted on gridded maps and later transferred to 1:30000 aerial photographs. Outermost sightings for individual warblers were joined to obtain territorial boundaries. Although at least eight visits are recommended for spot-mapping (International Bird Census Committee 1970), we believe our effort was sufficient because our primary interest was the presence/absence of warblers at a locality. In late June of both years, forest fragments unoccupied by male warblers were surveyed again to verify the absence of birds. At 50 m intervals, Black-and-white Warbler songs were played for 2 min, followed by 5 min pauses. No new warbler was detected during surveys, and because access to occupied areas within fragments took us regularly through unoccupied areas it is unlikely that we missed any territorial birds.

2) Vegetation sampling

Vegetation composition was measured in unoccu-

pied fragments (UNF), in occupied fragments both within (WTF) and outside territories (OTF), and within territories in contiguous forest. Vegetation was sampled between early and mid-July using a modification of the circular sampling plot method (James & Shugart 1970). At randomly selected plots within each site (e.g. an unoccupied fragment), we recorded species/genus and number, height (using a clinometer) and diameter at breast height (using a dbh measuring tape) of all trees (>1.75 m tall), shrubs (woody plants 0.5–1.75 m tall) species/genus and number, and maximum shrub height. At a vegetation plot, trees were sampled within an 11.2 m radius, but shrubs were sampled within a 5 m radius. Further, at 20 randomly-selected locations within an 11.2 m radius of a vegetation sampling plot, we recorded presence or absence of canopy (>5 m tall) and ground cover by looking through an ocular tube (4 mm in diameter) to estimate relative canopy closure and herb layer cover, respectively. Vegetation data were collected from 50 plots within 10 territories in four occupied fragments, 15 plots outside of territories in three occupied fragments, 20 plots within four unoccupied fragments, and 20 plots within four territories in contiguous forest. We assumed that vegetation changed little between years, therefore forest fragments were sampled only in 1993, except for one newly located territory in 1994.

We used multivariate analysis to compare vegetation composition within and among sites in the three forest fragments categories (UNF, WTF, OTF), and between territories in fragments and contiguous forest. Principal components analysis (PCA) was performed using CANOCO (ter Braak & Smilauer 1998)

based on the 27 variables listed in Table 1, all of which were square-root transformed to approximate a normal distribution. Preliminary inspection of the data using Detrended Correspondence Analysis produced gradient lengths <2, indicating that PCA was the appropriate ordination technique (ter Braak 1987). In order to determine whether habitat differed among the three occupancy categories in fragments and between territories located in fragments versus contiguous forest, multiple-response permutation procedure (MRPP), a non-parametric equivalent of discriminant analysis (PCORD; McCune & Mefford 1997), was performed on vegetation data.

3) Foraging behavior and habitat use

During May–June 1994, foraging data were collected for nine males in forest fragments and four males in contiguous forest. Individual warblers were observed weekly between 05:00 h and 12:00 h, on days without heavy rains or strong winds, for a total of 156 h. Each male was visited on six to eight dates. Males were located using vocalizations and then tracked for up to 90 min. Foraging data were collected by composing a timed, continuous record of an individual's movements until it was lost from view. When an individual was relocated, a new timed sequence began. While making observations, we also recorded foraging locations on gridded maps to validate territorial boundaries generated by spot-mapping.

We recorded: (1) species or genus of tree on which a foraging sequence (a series of movements that began when a bird landed on a plant and ended when it left) occurred (hereafter foraging tree), (2) sub-

Table 1. Vegetation variables measured from plots in forest fragments and a contiguous forest in central Alberta.

Category	Vegetation type
No. trees (woody plants >1.75 m tall)	Willow (<i>Salix</i> spp.), Trembling aspen (<i>Populus tremuloides</i>), Balsam poplar (<i>P. balsamifera</i>), White birch (<i>Betula papyrifera</i>), Alder (<i>Alnus</i> spp.), White spruce (<i>Picea glauca</i>)
Tree sizes	Mean tree height (m), Mean dbh (mm)
No. shrubs (woody plants 0.5–1.75 m tall)	Red-osier dogwood (<i>Cornus stolonifera</i>), Wild gooseberry (<i>Ribes oxycanthoides</i>), Wild red raspberry (<i>Rubus idaeus</i>), Honeysuckle (<i>Lonicera</i> spp.), Prickly wild rose (<i>Rosa acicularis</i>), Snowberry (<i>Symphoricarpos</i> spp.), Caragana sp., <i>Viburnum</i> spp., <i>Prunus</i> spp., Saskatoon berry (<i>Amelanchier alnifolia</i>), Maple sapling (<i>Acer</i> sp.), Balsam poplar sapling, Willow sapling, Trembling aspen sapling, Birch sapling
Shrub height (mm)	Mean maximum shrub height
Cover ^a	Canopy, Ground

^a See Methods for estimation of these variables.

strates where foraging attempts were made (see Table 2 for substrate categories), and (3) foraging method. Foraging methods observed were: glean (prey picked from substrate while perched), hawk (prey captured in mid-air while in flight), hover (prey picked from substrate while in flight without landing), and poke (bill inserted into a substrate to extract prey). Because Black-and-white Warblers usually feed on small prey (N. S. Sodhi, pers. obs.), we could not reliably determine the success of capture attempts, therefore, we treat all attempts equally as indicators of foraging effort.

We used Redundancy Analysis (RDA; CANOCO; ter Braak & Smilauer 1998) to assess patterns of foraging behavior (use of trees, substrates, and methods) of individual males within forest fragments and contiguous forest as constrained by habitat features of their territories. RDA is the appropriate form of direct gradient analysis to complement the indirect gradient analysis, PCA, that we previously chose for assessing vegetation patterns alone (ter Braak 1987). Frequency of occurrence of the behavioral categories described above were used to compare the total foraging records of nine territorial males from fragments with those of four males from contiguous forest. Vegetation data used in RDA were based on samples from five plots within each territory, and consisted of mean abundance of the five tree species where foraging was observed: alder, balsam poplar, trembling aspen, white birch, and willow. All values were square-root transformed. MRPP analyses of foraging data matrices were used to determine whether behavioral patterns differed significantly between warblers occupying territories in the two habitat types.

RESULTS

1) Habitat characteristics of forest fragments

Each year nine male Black-and-white Warblers occupied four (2, 50, 113, and 140 ha in area) of eight fragments. Occupied and unoccupied fragments remained the same in both years. Eight (89%) of nine territories found in 1993 were also occupied in 1994. In a given year, each transect encountered between one and four territories. Two of nine males in 1993 and four of nine males in 1994 fledged young (see also Sodhi & Paszkowski 1997).

In our analysis of vegetation composition, the first two principal component axes accounted for 48% of the variation among plots (30% and 18% for axis 1 and 2, respectively). On the ordination plot for PC

axes 1 and 2, the three categories of vegetation plots from forest fragments (WTF, OTF, UNF) were clearly aggregated (Fig. 1A). Vegetation composition differed significantly in pairwise comparisons between the three plot types (MRPP analyses: WTF vs. UNF, $P=0.000$; WTF vs. OTF, $P=0.000$; and OTF vs. UNF, $P=0.007$).

Strongly positive "species" scores on the first PC axis for willow and alder reflected the dominance of these plants within the overstory of territories in occupied fragments (Fig. 1A). The shrub layer on territories was characterized by raspberry and gooseberry. Negative scores on the first axis for trembling aspen trees and saplings coincided with high densities of this species in areas within occupied fragments but outside territories (Fig. 1A). Vegetation on unoccupied fragments was also characterized by a relatively high abundance of aspen and absence of willow. Shrub species composition, however, was most influential in distinguishing plots from unoccupied fragments, where the understory was dominated by dogwood, rose, and viburnum.

2) Characteristics of territories in contiguous forest versus fragments

Five males were located in the contiguous forest in 1994; three of these males successfully produced fledglings. In our comparison of vegetation characteristics of the territories of warblers located in contiguous forest versus territories in forest fragments, the first two PC axes accounted for 56% of the variation among plots (36% and 20% for axis 1 and 2, respectively). Plots differed distinctly between the two forest types (Fig. 1B), with the first axis separating samples from territories in contiguous forest versus fragments, and the second axis further separating territories within fragments. MRPP confirmed that vegetation profiles of territories in the two habitats differed significantly ($P<0.001$). As noted in the general analysis of vegetation patterns for fragments (Fig. 1A), territories were distinguished by willow in the overstory and by raspberry and gooseberry in the understory, reflected in negative scores for these species on the first PC axis. In contrast, high positive scores on axis 1 for trembling aspen trees reflected dominance of this species within territories in contiguous forest with viburnum and rose contributing to a tall shrub layer (Fig. 1B).

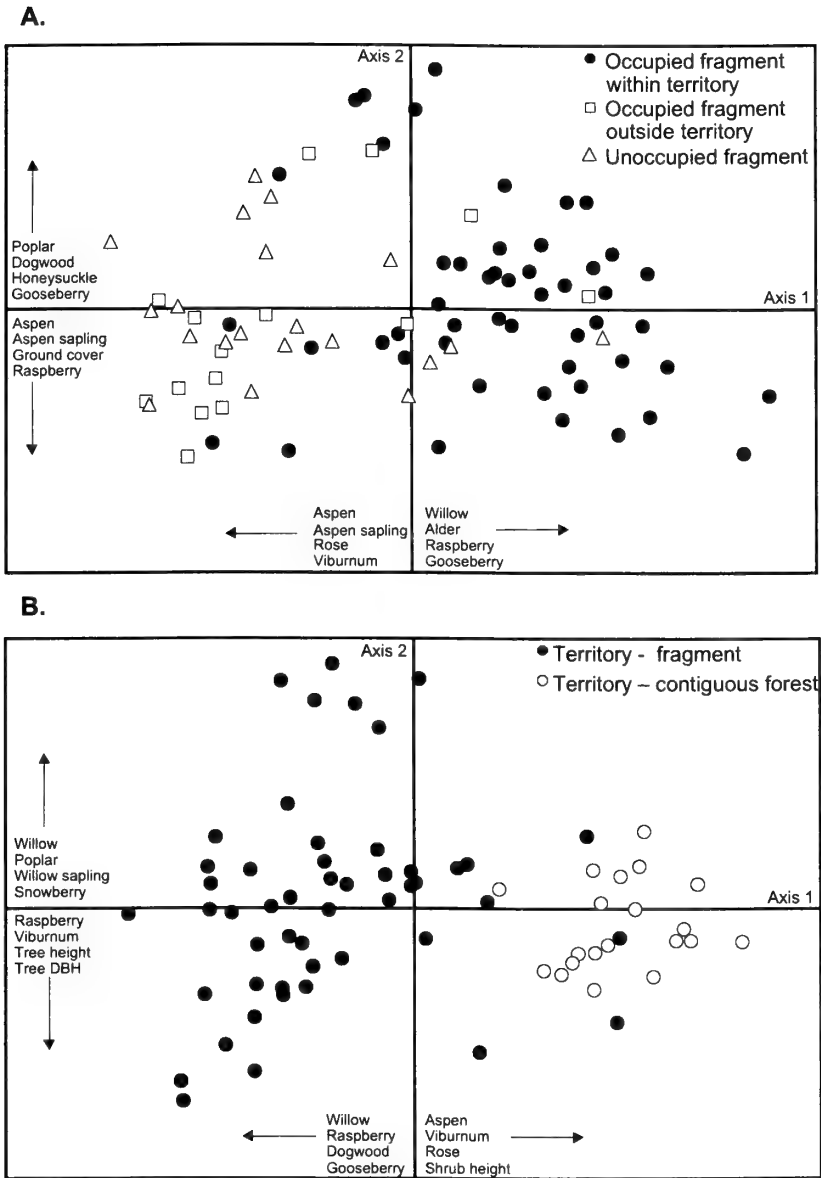


Fig. 1. Principal component analysis ordinations based on 27 vegetation variables (see Table 1), comparing habitat features of plots in aspen-dominated forest fragments (2–140 ha) that were not occupied by Black-and-white Warblers, plots outside territories in occupied fragments, and plots inside territories (A), and comparing habitat features between plots within territories in fragments versus within territories in an aspen-dominated contiguous forest (>1000 ha; B). Vegetation variables listed had the greatest positive or negative “species” scores on PC axis 1 or axis 2.

3) Foraging behavior in fragments versus contiguous forest

Of the three aspects of foraging behavior that we examined via multivariate analysis (use of tree species, substrate, and method), only use of foraging trees differed significantly between males on forest fragments and those in contiguous forest (MRPP; $P=0.001$). Thus only results from RDA examining

tree use are presented here (Fig. 2). The first and second axes explained 38% and 11%, respectively of the variation in foraging behavior among individuals. The constrained ordination separated birds occurring in contiguous forest versus fragments. Males in contiguous forest most commonly foraged on trembling aspen, whereas males in fragments favored willow and balsam poplar as foraging trees (see also Table

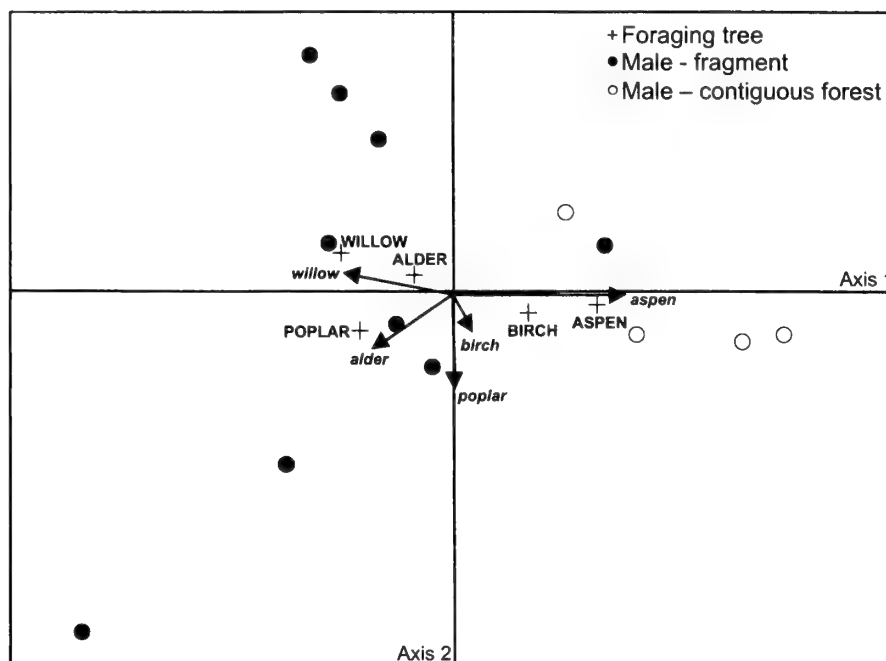


Fig. 2. Redundancy analysis triplot summarizing the use of tree species as foraging sites (crosses), behavior of individual birds (circles), and occurrence of these same tree species on territories (vectors) for 13 male Black-and-white Warblers in aspen-dominated forest fragments versus an aspen-dominated contiguous forest.

2). As indicated by the triplot, use of foraging trees paralleled the abundance of the five species in contiguous forest versus fragments.

Foraging method and foraging substrates did not differ between male warblers in forest fragments and contiguous forest (MRPP: substrate, $P=0.618$; method, $P=0.611$). In both habitats, birds captured prey mostly by gleaning, which accounted for 90% and 78% of all feeding attempts observed in fragments and contiguous forest, respectively (Table 2). The most frequently used foraging substrate was branches, the site of 47% and 37% of all attempts in fragments and contiguous forest, respectively (Table 2).

DISCUSSION

Black-and-white Warblers at the southern edge of the boreal forest in Alberta displayed distinct patterns of habitat use at several spatial scales and behavioral patterns that, in turn, reflected the composition of the defended forest patch. The species was not a specialist on forest-interior habitat as some authors have proposed (Freemark & Collins 1992; Morneau et al. 1999) and occupied half of the forest fragments surveyed. Occupancy was not dictated by patch size (the

smallest 2 ha fragment supported a territory), but was clearly related to finer scale vegetation patterns within individual patches. Several recent studies in the eastern United States have also shown the Black-and-white Warbler to be more variable in its habitat associations than previously described. Golet et al. (2001) and Lichstein et al. (2002) both reported that landscape features were important in determining the occurrence and abundance of the species at individual sites. The former study, for example, found that Black-and-white Warblers occurred in red maple (*Acer rubrum*) swamps as small as 1 ha in area if sufficient swamp forest was available in the larger landscape.

All fragments in our study were chosen based on a qualitative dominance of mature trembling aspen, yet the density of other woody species proved more important in determining if a particular fragment supported a warbler territory and where that territory was located. High densities of willow stems in the overstory characterized Black-and-white Warbler territories in these forest fragments. All 50 of the plots sampled within territories contained willow trees, with an average of 9 stems per plot. Areas in occupied fragments that were outside of territories actually supported higher densities of aspen trees and saplings

Table 2. Foraging behavior of male Black-and-white Warblers in forest fragments (2–140 ha; $n=9$ individuals) and contiguous forest (>1000 ha in area; $n=4$ individuals) in central Alberta. Values represent the mean and range of percentage of occurrence of foraging sequences (tree species) or prey attempts (substrate and method) associated with each variable from males from the two habitat types. (See Table 1 for scientific names of plants.)

	Forest fragments Mean (range)	Contiguous forest Mean (range)
Foraging tree		
Willow	50.7 (0–100)	15.6 (0–50)
Alder	5.4 (0–33.3)	0
Trembling aspen	10.0 (0–71.4)	63.7 (40–88.4)
Balsam poplar	20.5 (0–71.4)	20.6 (10–33.3)
White birch	0	13.4 (0–100)
No. of foraging sequences ^a	100	45
Foraging substrate ^b		
Trunk	17.0 (0–34.1)	24.3 (0–50)
Limb	6.1 (0–16)	5.7 (0–51.7)
Branch	56.9 (32–100)	35.5 (28.5–42.5)
Twig	12.6 (0–21.3)	19.4 (3.3–42.8)
Leaf	3.0 (0–9.1)	7.1 (0–13.3)
Air	4.0 (0–13.1)	13.2 (3.8–28.5)
Foraging method		
Glean	90.1 (77.7–100)	79.6 (71.4–92.3)
Hawk	4.1 (0–14.0)	11.5 (0–28.5)
Hover	1.4 (0–8.3)	4.6 (0–12.3)
Poke	3.3 (0–14.8)	7.1 (0–7.6)
No. of captures ^c	410	139

^a Foraging sequence defined as series of movements that began when a bird landed on a plant and ended when it left that plant.

^b Foraging substrates (after Sodhi & Paszkowski 1995): trunk = wood >12 cm diameter, limb = wood 2.6–12 cm diameter, branch = wood 1.0–2.5 cm diameter, and twig = wood <1 cm diameter.

^c Number of prey captures was used to calculate the percentage use of both foraging substrates and methods.

than areas inside, but willow was virtually absent, with only one tree encountered in 15 plots. Dominance by trembling aspen, but with a decline in willow and a change in the composition of the shrub layer, typified the four unoccupied fragments. Ordination indicated that the two categories of “unoccupied” plots were more similar to each other in vegetation composition and structure than either was to plots within territories. It is of interest that plant species composition appeared to affect occupancy patterns of forest fragments more than did broader structural features of the canopy, shrub layer or

ground cover. Although our results cannot elucidate the specific causes behind this pattern for Black-and-white Warbler, Whelan (2001) demonstrated experimentally for three other species of wood warbler that the foliage structure of different deciduous tree species created distinctive foraging microhabitats that influenced warbler behavior.

Based only on results from forest fragments, we might conclude that willow thickets offer preferred conditions for breeding Black-and-white Warblers in a boreal mixedwood setting. Yet when plots from territories in fragments are compared with vegetation samples from within territories in contiguous forest, the species’ patterns of habitat use become more complex (Fig. 1B). In the contiguous forest tract, results more closely matched expectations for habitat preferred by Black-and-white Warblers in north-central Alberta derived from other studies (e.g. Schieck et al. 1995; Hobson & Schieck 1999), i.e., the most distinguishing feature within territories was a dominance of large and small trembling aspen. Aspen trees were present in 95% of the plots within territories, and willows in only 60%; plots that did contain willow averaged only 3.4 stems per plot.

In turn, in contiguous forest and fragments, males used the dominant tree species as their primary foraging site, aspen and willow respectively (Fig. 2). Different tree species typically harbor different invertebrate prey, or differ in the abundance or accessibility of shared prey types (Robinson & Holmes 1982; Holmes & Schultz 1988; Adams & Morrison 1993; Whelan 2001). Other studies have reported that bird species may or may not respond to shifts in plant species composition by using different foraging tactics in different habitat settings (Franzreb 1983; Block 1990; Petit et al. 1990; Miller & Cale 2000). We found that the use of aspen versus willow was the only behavior of Black-and-white Warblers that differed significantly between the two habitats, and basically mirrored tree availability (Table 2). Foraging followed the pattern typical of wood warblers, with a predominance of simple gleaning and some use of flight, a tactic that was somewhat more common in contiguous forest. Males displayed the species’ peculiar nuthatch-like behavior on both aspen and willow, with about one third of all prey captures occurring on larger diameter limbs and trunks where birds occasionally probed into bark for prey. The foraging methods of the Black-and-white Warbler may be appropriate for a variety of habitats and lend the species considerable versatility in the types of forest that it

can occupy even within a single geographic region (Lichstein et al. 2002). Strong (2000) reported a similar situation for over-wintering Ovenbirds (*Seiurus aurocapillus*) in the West Indies. This species' ground foraging behavior, which focuses on capturing ants and is unusual for a wood warbler, allowed it to use a surprisingly diverse number of habitat types.

The key distinction that we found between Black-and-white Warblers inhabiting human-created fragments and birds inhabiting a larger, contiguous forest tract was the strong link between warblers and willows in fragments. One explanation for this pattern is that warblers were selecting for particular features other than dominant tree species when choosing fragments and establishing territories therein, and those other features were incidentally associated with willows. The warblers' foraging techniques allowed them to feed on willows as the most commonly encountered component of the overstory vegetation. We documented, for example, strong differences in the abundance of a variety of shrub species between habitat types and in areas inside versus outside territories. Black-and-white Warblers are ground nesters. The structure and composition of the shrub layer might affect habitat selection by shaping nest cover and microhabitat conditions, and affecting the likelihood of predation or parasitism (Martin & Roper 1988; Steele 1992; Ricketts & Ritchison 2000). Warblers might be establishing territories to encompass suitable nest sites.

A second explanation for the observed linkage is that Black-and-white Warblers actively select fragments with willows because these trees are exceptionally good foraging sites (based on arthropod abundance or delectability) and occur more densely embedded within open aspen stands. An abundance of willows can perhaps compensate for other shortcomings of forest fragments as breeding sites (e.g. higher risk of nest predation). In a previous study (Sodhi et al. 1999), we reported a similar strong association between American Redstarts (*Setophaga ruticilla*) and willows in some of the same mixedwood fragments. Bisson and Stutchbury (2000) reported that Hooded Warblers (*Wilsonia citrina*), a species often characterized as requiring large areas of mature forest, inhabited and had good breeding success in woodlots that contained a dense understory. They suggested that, at a finer spatial level, Hooded Warblers in mature stands might similarly be attracted to scattered canopy gaps associated with well-developed shrub layers. We found that all Black-and-white War-

bler territories in the contiguous forest contained some willow as well. Nonetheless, even in fragments, dependence on willow as a foraging site was not absolute as one of nine males was never seen foraging in willow and three additional males used other plant species more frequently.

In summary, our study suggests that the Black-and-white Warbler will nest in relatively small patches of forest in the boreal mixedwood ecoregion. Warblers do not, however, behave as if these fragments were scaled-down versions of undisturbed stands. Different features of the vegetation determine where males establish territories, and to some extent, males adopt different foraging tactics. In short, birds in fragments "adjust" to local conditions. Like the Black-and-white Warbler, many species of North American forest passerines have wide ranges, but nowhere are they particularly common. Their biology undoubtedly varies across the continent, but is seldom documented because studies (such as ours) of these species in specific ecological settings will be based on data from relatively few individuals. If we wish to learn about these species, and not be content with limiting research to very common or very rare species, or making faulty generalizations about the ecology of uncommon species, we must acknowledge and accept the logistical constraints inherent in such studies.

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ORIGINAL ARTICLE

Estimation of hearing range in raptors using unconditioned responses

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Abstract We developed a new method to estimate the auditory abilities of animals using responses elicited by the presentation of auditory stimuli, without restraining or training the subjects. Using this method, we examined the hearing ranges of four raptors (a Mountain Hawk-eagle *Spizaetus nipalensis*, Northern Goshawk *Accipiter gentilis*, Common Buzzard *Buteo buteo*, and Grey-faced Buzzard-eagle *Butastur indicus*) kept in Ueno Zoo, in Japan, by presenting pure tones and white noise at two sound-pressure levels. Unconditioned responses, such as pupillary dilation and physical movements, were observed in all subjects. We then presented paired video clips of the raptors, with and without auditory stimuli, to human assayers, who were asked which clip contained the auditory stimulus. The accuracy of the human perceptual assay (HPA) suggested that the Mountain Hawk-eagle and Northern Goshawk hear frequencies from 1 to 5.7 kHz best, which is comparable to the results of an experiment with an American Kestrel *Falco sparverius* and European Sparrowhawks *Accipiter nisus*. The assayers reported that they used movements of the neck, head, and eyes, and changes in the pupils of the raptors as critical cues. Our method reliably reflected the hearing ranges of the raptors, and should be helpful for estimating the auditory capabilities of rare animals, such as the Mountain Hawk-eagle studied here.

Key words Hearing range, HPA, Raptors, Unconditioned response

Hawks and eagles, which belong to the order Falconiformes, are diurnal birds that hunt insects, birds, and small mammals, such as rabbits, voles, and mice. They usually sit on high perches, and dive at high speed when they attack prey. Therefore, they are strongly dependent on their excellent visual capacity when hunting. Their excellent visual ability is supported by the evidence that some raptors have much bigger eyes than humans, relative to their body size, and much greater visual acuity than humans (e.g., Wedge-tailed Eagle *Aquila audax*, Reymond 1985).

Auditory stimulus is also important for raptors, because it indicates that prey is approaching or that it is

alarmed against them (Klump et al. 1986), that it is dangerous advance, or that hatchlings/fledglings are hungry, and so on. Few studies, however, have examined the auditory abilities of Falconiformes, which do not appear to be exceptional among avian species (Fig. 1). Trainer (1946) measured hearing in the American Kestrel *Falco sparverius* using conditioned responses elicited by, or emitted in response to, electric shocks that were preceded by pure tones. He showed that the kestrel responded to sounds at frequencies of 1–4 kHz. Klump et al. (1986) measured the audible range of European Sparrowhawks *Accipiter nisus* using discrimination training through an operant conditioning technique, and found that the hawks were most sensitive to sounds from 1 to 4 kHz. Their best frequency was 2 kHz, while they could not

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ear sounds at frequencies higher than 8 kHz. This hearing range is average in relation to birds in general, but is much narrower than that of owls and some other raptors (Dyson et al. 1998). The differences in the hearing abilities of these birds likely evolved because hawks are diurnal and they catch their prey from great distances using visual cues, whereas owls are nocturnal and they catch their prey from short distances using auditory cues.

For conservation purposes, it is necessary to know the auditory capabilities of raptors, especially those living in forested or mountain habitats, because such birds are often affected by human habitat-alternating activities such as logging, dam construction, and residential developments. Noise from these projects may influence the birds' reproductive or foraging success. Therefore, we need to be able to identify noise levels and understand how such noise might affect raptors.

Unfortunately, we do not have sufficient data on the auditory ability of raptors, mainly because many of their populations are endangered, which makes it impossible to undertake experiments that require surgery or long periods of time for the collection of data, such as electrophysiological studies and operant discrimination training. Therefore, in order to determine the auditory capabilities of raptors, we must develop non-invasive methods that can be completed over short periods.

One solution is to use unconditioned responses to sound. For example, Megela-Simmons et al. (1985) used a "reflex modification" technique to obtain audiograms of the Bullfrog *Rana catesbeiana* and Green Tree Frog *Hyla cinerea*. In their technique, the unconditioned reflex elicited by the electric shock was inhibited when the pre-stimulus, say, pure tone, preceded the presentations of the shock if the animal had detected the pre-stimulus. The audiograms measured by reflex modification technique agreed well with neural sensitivity data (Ehret & Capranica 1980; Shofner & Feng 1981). Recently, Bala and Takahashi (2000) measured the hearing curve in American Barn Owls *Tyto alba* using the pupillary dilation response elicited by the presentation of sound, and found that it was consistent with the data that Quine and Konishi (1974) obtained using operant conditioning. Although methods using unconditioned responses to sound have marked advantages over the operant conditioning method in that they do not require prior training, the subjects must be restrained during these experiments, and aversive stimulus or surgical operation is necessary to obtain small behavioral changes.

Here, we establish a method of estimating the hearing ability of unrestrained, captive raptors using responses to sound presentation, such as pupillary dilation, blinking, orienting responses, and small movements of the body. The subjects were four Japanese raptors (a Mountain Hawk-eagle *Spizaetus nipalensis*, Northern Goshawk *Accipiter gentilis*, Common Buzzard *Buteo buteo*, and Grey-faced Buzzard-eagle *Butastur indicus*) kept in a zoo. We assumed that unconditioned responses would be observed only when sound was presented, and that such responses could be used as an index of hearing. We videotaped the behavior of the raptors with and without sound presentation, and then asked human assayers who were unaware of the experimental conditions to judge whether a given video clip contained sound presentation. We called this the Human Perceptual Assay (HPA). We assumed that if the assayers could correctly categorize the clips using responses to sound presentation as discriminative cues, the HPA would then reflect the hearing capability of the raptors.

MATERIALS AND METHODS

1) Study Area

Two experimenters recorded the raptors' behavior on days when Ueno Zoo, Tokyo, was closed to the public, from 16 March 2001 to 9 July 2001. One experimenter controlled the stimulus presentation, and the other videotaped the behavior of the subjects. Two loudspeakers were placed just in front of the birds' metal cage, and the video camera was set at least 3 m behind the loudspeakers. The distance between the loudspeakers and the birds was 3 to 6 m. The sound pressure levels were adjusted for distance so that they were equal where the birds were.

After the recording, we conducted the HPA in a laboratory at Chiba University.

2) Subjects

The subjects were four raptors kept in Ueno Zoo: a male Mountain Hawk-eagle, a male Northern Goshawk, a male Common Buzzard, and a Grey-faced Buzzard-eagle of unknown sex. The Mountain Hawk-eagle had been shot in the wild and taken to the zoo; it had recovered and was flying freely in its cage at the time of the experiment. It was kept in a cage by itself. The wings of the Northern Goshawk and Common Buzzard had been injured, and neither bird could fly; these two hawks were kept in a cage

with five Ural Owls *Strix uralensis*. The Grey-faced Buzzard-eagle could fly, and lived with two Common Kestrels *Falco tinnunculus*.

Three male volunteers (22–30 years-old) took part in the HPA as assayers.

3) Materials

The auditory stimuli were controlled by a CD player (SL-SW404, Panasonic) and broadcast from two loudspeakers (YST-M100, Yamaha). The behavior of the raptors was recorded with a digital video camera (VL-MR1 PRO, Sharp). We used a personal computer (PCV-J15, Sony) and video presentation software (Adobe Premiere 5.1 for Windows, Adobe) for the HPA.

4) Stimuli

The sound stimuli were created using Avisoft-SAS Lab Pro software (Avisoft) with a sampling frequency of 44.1 kHz. The stimulus duration was 0.8 sec with rise-fall times of 50 ms. We prepared pure tones at eight different frequencies (0.25, 0.5, 1, 2, 4, 5.7, 8, and 11.3 kHz) and white noise. The frequencies of the pure tones were determined using the octave scale, except for 5.7 kHz, which was the geometric mean between 4 and 8 kHz. Each sound had two sound pressure levels, 50 ± 4 dB and 74 ± 4 dB, and the difference between the two levels was 24 dB.

5) Procedure

Sound presentation and video recording of the hawks The test sounds were presented from in front of the cage when the birds were not moving and there was relatively little external noise. The sounds were presented using the constant stimuli method (Klump et al. 1995); i.e., the stimuli were presented in random sequences within and among sessions. The inter-stimulus interval was at least 30 sec, and it was usually much longer, either because the birds were moving or there was external noise. The sound and no-sound conditions were alternately presented after the inter-stimulus interval. In the sound condition, we presented an auditory stimulus 3 seconds after pushing the button on the CD player. The procedure in the no-sound condition was the same as in the sound condition, except that no sound was broadcast. We videotaped mainly the upper part of each bird, including the head, shoulders, and abdomen, in these sessions. A session consisted of 18 sound conditions, which consisted of one sound at each of the nine frequencies and two sound-pressure levels, and 18 no-sound con-

ditions. Experiments were conducted on three separate days for each subject, with one session per day. Therefore, 54 video clips with sound and 54 clips without sound were obtained for each subject.

HPA To determine whether the birds responded to the sound stimuli and not to the no-sound condition, we conducted the HPA. In the sound condition, the original video records were edited so that in a 4.8-sec video clip, the sound presentation period was in the middle 0.8 sec of the clip. A 4.8-sec clip of the no-sound condition was edited similarly. Two video clips, one from the sound condition and the other from the no-sound condition, were randomly paired and presented to the assayers of the HPA in windows on each side of a PC monitor, without any auditory information. Before the assay, we told the assayers five things:

1. Look carefully at the video clips presented on the left and right sides of the screen, one at a time;
2. Each clip contains a raptor, and is about 5 seconds long;
3. In one clip, a sound was played to the hawk for about half the length of the clip; no sound was played in the other clip;
4. Determine which clip contains the sound;
5. After the presentation, check the blank space with the corresponding trial number on your response sheet using a pencil.

Note that because the assayers were not told about critical cues that might suggest the presentation of the sound, they were free to use any cues in the clips to make their decision.

Before presenting the test clips to each assayer, eight training trials were run using video clips that were not used in the subsequent test session: four each from the sound and no-sound conditions. In the training session, the clips in the sound condition contained obvious behavioral changes to ensure that the assayers understood their task. During training, the assayers were shown one clip per trial, and were asked to answer yes or no to whether the clip contained a sound presentation. The researcher gave feedback (correct or incorrect) after each answer. The sequence of the trials was such that the same condition (sound or no-sound) was not repeated more than three times in a row. The assayers had more than 50% correct responses to each bird condition. The training session was only given once regardless of how the assayers performed.

In the test session, clips were presented on the left

at the left sides of the monitor in each trial. In one clip, sound was presented to the bird, and in the other it was not. The conditions (sound or no-sound), positions of the clips (left or right), and the starting clip of a given trial (left or right) were determined using quasi-random sequences, in which the same conditions were not repeated more than three times in a row. One block consisted of 18 trials, which included nine different sound conditions at two sound-pressure levels, and 18 clips from the no-sound condition. These clips were selected from the three separate experiments for each raptor. A session consisted of six blocks, and the 54 different clips were presented twice; therefore, 108 trials per session were run. The assayers were given all three test sessions, one for each raptor with a different sequence of trial blocks, and the orders for the four raptor species were counterbalanced among the assayers.

After the HPA trials, the assayers were asked the following questions:

1. What were the critical cues or rules they used in making their decisions?
2. Were there distinctive characteristics or consistent changes in the behavior of the different raptors?
3. How difficult was it to make a decision, and what was your general impression of the tasks?

Calibration Calibration was performed by placing a sound-level meter with a 1/3 octave band filter at 3, 5, and 6 m from the loudspeaker. These were the distances at which the birds perched during the experiment. Ambient noise level was also measured at the same distances for each 1/3 octave. For the 250-Hz test frequency, some of the harmonic distortion products were as intense as 10 dB below the fundamental. Therefore, the data for the 250-Hz tone was excluded from further analyses. For the other test frequencies, harmonic distortion within the audible range (assuming 15 kHz at most) was at most 30 dB below the fundamental at each test frequency for each harmonic. The 1/3 octave noise level was converted into a spectrum level by subtracting the logarithm of the bandwidth. The signal level was at least 50 dB above the ambient noise. This suggests that no masking occurred at the test frequencies, and that the thresholds obtained here reflect true, unmasked thresholds.

6) Statistics

We calculated the response accuracy of three as-

sayers in each bird condition for each sound condition (Fig. 2). The average accuracy of the HPA was calculated for the three assayers in the six trials for each sound condition, in which each raptor condition was presented once per block. The accuracy at frequencies of 1 to 4 kHz was calculated separately (upper panel of Fig. 3), because it is assumed that the raptors can hear sounds at these frequencies (Fig. 1; Trainer 1946; Klump et al. 1986). Consistency of the decisions made by the assayers was also calculated at these frequencies to determine whether they used the same cues for their decisions in each trial. If all the assayers made the same decision (sound presence or absence), then it was counted as 1. If there was a difference among the decisions, then it was counted as 0. We performed a binomial test to examine the difference between the accuracy or consistency and expected value. The chance level was set at 0.5 for accuracy, and 0.25 for consistency. To examine the difference of the accuracy and the consistency among birds, one-way analysis of variance (one-way ANOVA) was conducted, and then Tukey's HSD test was used for multiple comparisons. In addition, we calculated the kappa κ to measure the agreement of the judgment by the assayers (Siegel & Castellan 1988).

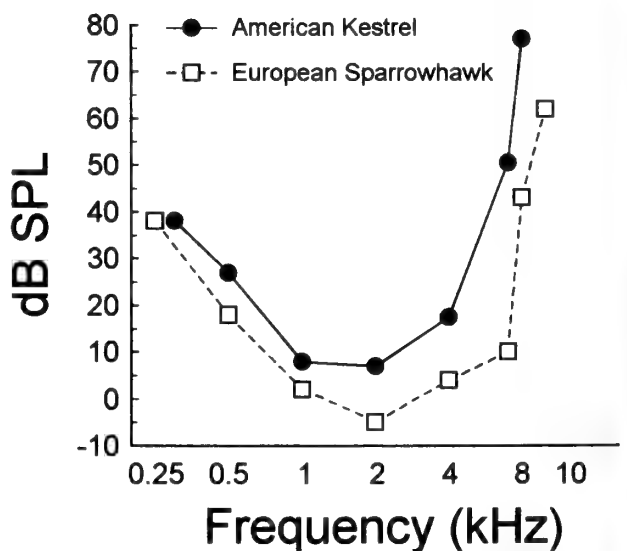


Fig. 1. Audiograms of the American Kestrel (Trainer 1946) and European Sparrowhawk (replotted from Klump et al. 1986).

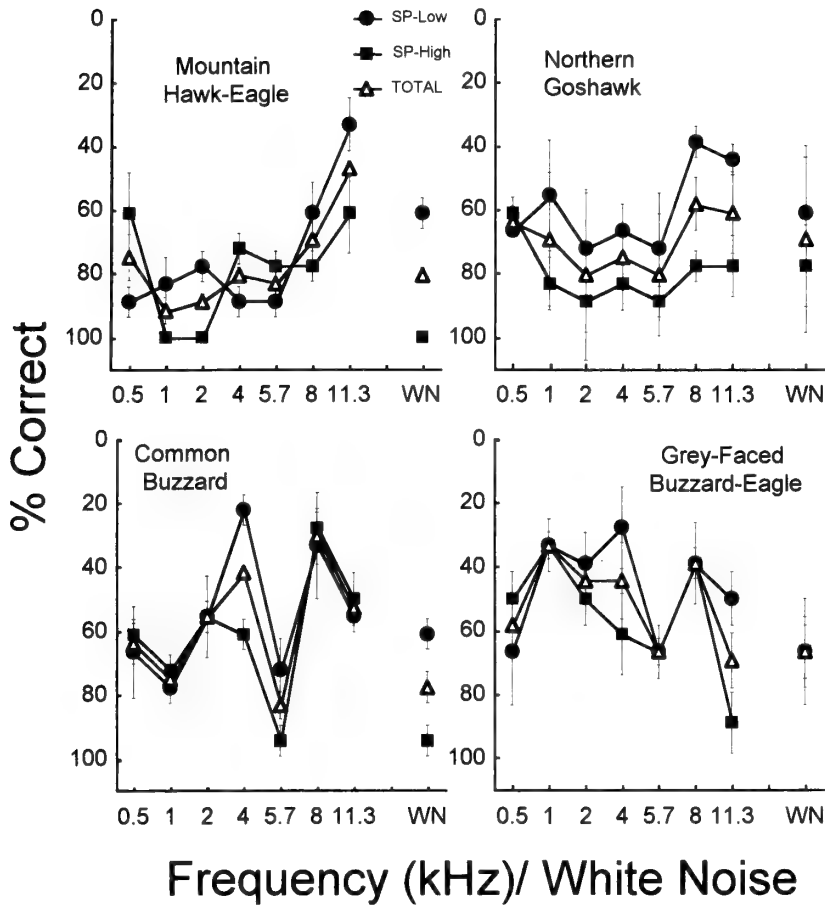


Fig. 2. Response accuracy of the human perceptual assay (HPA) of raptors, with SD. The numbers and letters on the horizontal axis represent the sound frequency and white noise (WN) presented to the raptors. There are separate plots for the low- (SP-Low) and high- (SP-High) pressure levels, and total (TOTAL), which was calculated regardless of the sound-pressure level. Note that the vertical axis is reversed (the origin is at the top of the y-axis) to compare the shapes of the curves with audiograms obtained in other studies (Fig. 1).

RESULTS

The average accuracy was calculated for the total and the two sound-pressure levels (Fig. 2). The total accuracy for the Mountain Hawk-eagle was 77.1%, for the Northern Goshawk 69.1%, for the Common Buzzard 60.1%, and for the Grey-faced Buzzard-eagle 52.8%. Comparison between the accuracy of the HPA at frequencies of 1 to 4 kHz and the chance level probability (upper panel of Fig. 3) revealed a significant difference for the Mountain Hawk-eagle (87.0%, $N=108$, $z=7.60$, $P<0.01$) and for the Northern Goshawk (75.0%, $N=108$, $z=5.10$, $P<0.01$), but not for the Common Buzzard (57.4%, $N=108$, $z=1.44$, $P>0.05$) or Grey-faced Buzzard-eagle (40.7%, $N=108$, $z=1.83$, $P>0.05$). There was a significant difference among the birds ($N=12$, $F=9.25$,

$df=3$, $P<0.01$), and following multiple comparison revealed that there was significant difference between the Grey-faced Buzzard-eagle and the Mountain Hawk-eagle ($N=3$, $P<0.01$), and the Northern Goshawk ($N=3$, $P<0.05$).

The assessment of the assayers (Fig. 2) was that they were 80% accurate for sounds at frequencies of 1 to 5.7 kHz in the Mountain Hawk-eagle, in both sound-pressure conditions. There is a steep decrease in accuracy from 5.7 to 11.3 kHz under low sound-pressure conditions, and from 8 to 11.3 kHz under high sound-pressure conditions. For the Northern Goshawk, the accuracy level of HPA was more than 80% from 1 to 5.7 kHz, but only under high sound-pressure conditions. The difference in the human performance between the sound-pressure conditions was clearer for this bird than for any of the other three

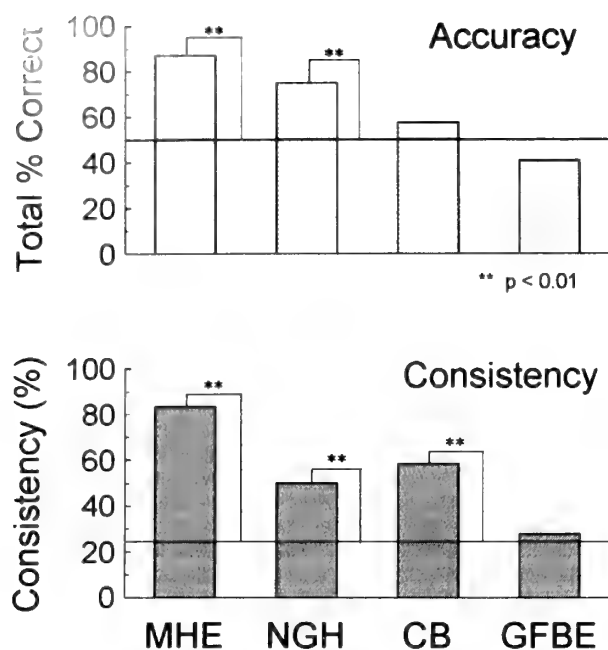


Fig. 3. Response accuracy (upper) and consistency (lower) of the three human assayers in the HPA of each raptor (MHE: Mountain Hawk-eagle; NGH: Northern Goshawk; CB: Common Buzzard; GFBE: Grey-faced Buzzard-eagle). The data were collected from the responses to the video clips with sound frequencies of 1, 2, and 4 kHz. In the upper panel, the solid line indicates the chance level of performance (50%). Consistency means the percentage of trials in which all three assayers made the same decision (sound presence/absence). The solid line indicates the chance level (25%). Asterisks indicate statistically significant differences between the data and a given chance level.

raptors. Under the low sound-pressure condition, the accuracy did not reach 80% at any frequency. The shapes of the curves obtained from the HPA of these two species were similar to those of the audiograms in Trainer (1946) and Klump et al. (1986).

By contrast, the performance in the HPA for the Common Buzzard and Grey-faced Buzzard-eagle (Fig. 2) oscillated markedly, depending on the sound frequency. In the Grey-faced Buzzard-eagle, the greatest accuracy under the high sound-pressure condition was for 11.3-kHz, the frequency at which the humans were not so accurate for the other three raptors. For the Common Buzzard, it was the highest for 5.7 kHz, and the lowest for 8 kHz. In these two birds, no consistent change in accuracy was observed with sound condition, for either frequency or sound pressure level.

Except for the Grey-faced Buzzard-eagle, the accuracy in response to the white noise condition was

comparatively high, and for the higher sound-pressure level it increased to around 80%.

The interviews of the assayers after the HPA experiment revealed that all of them used movements of the neck, head, and pupil, blinking, and behavioral changes seen in the video clip as cues for their decisions. Although the Mountain Hawk-eagle was not generally active, the assayers reported that its behavior changes were the most distinct of the four species, and one assayer noticed whether it blinked with one or both eyes. In the Northern Goshawk, two of the assayers reported that they divided the video clips into two categories based on the distinctiveness of the behavior changes. In the Common Buzzard, all of the assayers had difficulty detecting pupillary changes, because the border between the pupil and the iris is not clear in this species.

The consistency of the decision among the assayers (lower panel of Fig. 3) was above chance level (25%) in the Mountain Hawk-eagle (83.3%, $N=36$, $z=7.89$, $P<0.01$), the Northern Goshawk (50.0%, $N=36$, $z=3.27$, $P<0.01$), and the Common Buzzard (58.3%, $N=36$, $z=4.43$, $P<0.01$), but not in the Grey-faced Buzzard-eagle (40.7%, $N=36$, $z=0.19$, $P>0.05$). The difference among them was significant (one-way ANOVA, $N=24$, $df=3$, $F=9.96$, $P<0.01$). Further comparison between each species revealed that the consistency of the Mountain Hawk-eagle was higher than that of the Northern Goshawk (Tukey's HSD test, $HSD=1.73$, $N=6$, $P<0.05$), and the Grey-faced Buzzard-eagle ($N=6$, $P<0.01$), and that of the Common Buzzard was higher than that of the Grey-faced Buzzard-eagle ($N=6$, $P<0.05$). Thus, it was clear that both the response accuracy and consistency were high for the Mountain Hawk-eagle, whereas they differed for the Northern Goshawk and the Common Buzzard (higher response accuracy and lower consistency in the former, and they were reversed in the latter). By contrast, both of them were lower in the Grey-faced Buzzard-eagle. Kappa statistic also showed the same trend, that the agreement of the judgment was significantly above chance for the Mountain Hawk-eagle ($\kappa=0.51$, $z=2.18$, $P<0.05$) and Common Buzzard ($\kappa=0.43$, $z=4.30$, $P<0.01$), but not for the Northern Goshawk ($\kappa=0.11$, $z=0.76$, $P>0.05$) or the Grey-faced Buzzard-eagle ($\kappa=0.01$, $z=0.09$, $P>0.05$).

DISCUSSION

This study showed that the responses of the raptors

to sound presentation and the accuracy of our HPA could be used to measure their hearing ranges. The validity of our method was suggested by the similarity between the response accuracy to the Mountain Hawk-eagle and Northern Goshawk and the audiograms obtained in the prior experiments. The American Kestrel and European Sparrowhawk heard frequencies from 1 to 4 kHz best (Fig. 1), and the response accuracy of the HPA in the Mountain Hawk-eagle and Northern Goshawk was greater to sounds from 1 to 5.7 kHz (Fig. 2). In addition, the Mountain Hawk-eagle and Northern Goshawk showed clear and consistent responses to sounds within that range, as suggested by the performance that was significantly different from chance in those species. The high accuracy and consistency in HPA in the Mountain Hawk-eagle suggest that the assayers used the same behavioral cues that were well coincident with the sound presentation and had small variability. By contrast, in the Northern Goshawk, although all the assayers reported that it was easy to detect behavioral changes in this species, the high accuracy with lower consistency than that of the Mountain Hawk-eagle suggests that the assayers used the various behavioral cues that coincided with the sound presentation. It is possible that the Northern Goshawk was more sensitive to the sound stimuli than any of the other species. Assuming that there should not be a big difference in the auditory abilities of these species of raptor, the audibility range was from 0.5 to 8 kHz, with the best hearing range from 1 to 6 kHz.

This study might be criticized on the basis that the hearing ability of the raptors may not be identical with the response accuracy in the HPA. We also admit that our methodology cannot be used in all cases. Our observations indicated that the behavioral changes in response to sound presentation in the Common Buzzard and Grey-faced Buzzard-eagle were inconsistent. These birds often moved actively after being presented with sounds at frequencies of 8 or 11.3 kHz, which are reported to be beyond the hearing range of European Sparrowhawks (Klump et al. 1986), whereas they did not respond to sounds at 1 or 2 kHz, which are thought to be within their ranges. This inconsistency in their responses is why the performance of the HPA for these species was not statistically different from chance. By contrast, the Mountain Hawk-eagle and Northern Goshawk consistently showed behavioral changes to the sounds, and this was reflected in the higher HPA performance (upper panel of Fig. 3). The reasons for these differences

may be owing to the native habitats of these species. Mountain Hawk-eagles and Northern Goshawks usually perch in trees while foraging and roosting, whereas Common Buzzards and Grey-faced Buzzard-eagles live and hunt in open fields in flatlands. The former two species would be more used to hearing sounds distorted by obstacles than the latter two species. In the present experiment, pure tones were broadcast from speakers set in front of each bird's cage. Thus, it is possible that the tones were more strange to the Mountain Hawk-eagle and the Northern Goshawk than to the Common Buzzard and the Grey-faced Buzzard-eagle, and that they would be more sensitized. In addition, such habitat conditions would affect their movements on hearing the sounds. Mountain Hawk-eagle and Northern Goshawk may move actively in order to detect environmental changes visually, whereas Common Buzzard and Grey-faced Buzzard-eagle may move inactively in order not to be seen by preys in flatlands. Since our method relies on unconditioned responses to sound, it is not useful for species with small or few behavioral changes, such as Common Buzzards and Grey-faced Buzzard eagles. It is necessary to consider the specific ecology and behavior of the subject before applying our method. To confirm the hypothesis outlined above, we must increase the number of subjects to determine the generality of the behavioral characteristics to the sound observed in this study.

One could argue that the birds kept in a zoo may have become de-sensitized or habituated to certain auditory stimuli because they are continuously exposed to the sounds made by visitors. However, the pure tones used in the present study do not exist in a natural environment, and it was presumed to be the first time for the birds to hear these sounds. Additionally, the coincidence of the behavioral change with the sound presentation frequently observed in the subjects, precluded the possibility of loss of sensitivity to such kind of sounds.

Because the raptors other than the Mountain Hawk-eagle were kept in their cages together with other birds such as owls which are known to have greater sensitivity to the sound than hawks, consideration must be given to the fact that the subject birds could have used their behavioral changes to the sounds. However, such an effect would have been small, because the Common Buzzard, which showed inconsistent behavioral changes to the sounds, was kept in the cage with the Northern Goshawk which proved to be more sensitive than the buzzard.

We cannot say that the function (Fig. 2) represents the absolute hearing threshold in these raptors. However, the accuracy curve of the HPA measured using two different sound-pressure levels could be considered an equal-loudness curve for the raptors, reflecting the audible range under given conditions. By running additional tests using sounds at the best-heard frequencies and different sound-pressure levels, we should be able to estimate other auditory properties, such as absolute thresholds and frequency cutoffs.

In conclusion, our method is useful for estimating the hearing ranges of some raptors, and does not require training or restraints. The accuracy of the HPA reflected the hearing ranges of the birds. In addition, because we presented the sounds in front of the birds' usual cages, the possible effects of interference should have been minimal. Our method can be applied to animals in captivity and possibly even to those in the wild.

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We thank the staff of Ueno Zoo for their assistance over the course of this study. This study was supported by the Research on Conservation Techniques Program of the Ministry of Land, Infrastructure, and Transport of Japan. Portions of this paper were presented to the meeting of the Technical Committee of Psychological and Physiological Acoustics in 2001 in Chiba University, Japan, and at the 4th International Symposium on Physiology and Behaviour of Wild and Zoo Animals in 2002 in Berlin, Germany. We also thank the various referees for their critical comments on the manuscript.

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Abstracts of the Japanese Journal of Ornithology, Volume 52

Number 1

REVIEW

Egg production and its physiological regulation in domestic fowl.

Kiyoshi IMAI

Domestic fowl, *Gallus gallus domesticus*, is the most important poultry (domesticated birds that serve as a source of egg or meat to human beings) in the world. The process of egg production in the female bird is composed of follicular rapid growth in the ovary, ovulation of the largest follicle, egg formation in the oviduct and oviposition. In the present review, the ovipository pattern, the egg producing process and its physiological regulation, especially endocrine control, in the hen are described. The period required to follicular rapid growth is 8 days with a highest frequency, ranging from 7 to 10 days in almost all the follicles examined. Ovulation of the largest follicle in the ovary is mainly controlled by pituitary LH and follicular progesterone. Egg formation, being constituted by egg white, shell membrane and egg shell

surrounding yolk, is conducted in the oviduct during about 24 hours. Vasotocin and prostaglandins play an important role participating in oviposition.

Jpn J Ornithol 52: 1–12. 2003.

ARTICLES

Mate Guarding in the Black-faced Bunting *Emberiza spodocephala*.

Akira KOIWAI

The overlap of home ranges, copulation and mate guarding behaviour were studied in socially monogamous Black-faced Buntings *Emberiza spodocephala* from April to July in 1992 at Sugadaira (36°32'N, 138°20'E, 1,250 m alt). Each male bunting had a stable home range and a song area within that. Since males frequently intruded into neighbouring home ranges to seek extra-pair copulations, the home ranges overlapped greatly. Song areas also overlapped with each other. Once males acquired mates, they did not sing frequently. These suggest that males did not maintain the song area as a territory after pair formation. Males guarded their mates by spending

uch time near their mates and by following them closely. The shortness of intra-pair distance and the percentage of flights in which the female was followed by her mate peaked during the presumed fertile period. Males started mate guarding soon after pair formation. All 29 intra-pair copulations were observed during the fertile period. Aggressive behaviors between males due to attempts of extra-pair copulation were observed between pair formation and the fertile period. The half of 10 extra-pair copulations were observed during the fertile period. It means that males could not defend their mates completely. These results suggest that male Blackfaced Buntings guard their mates rather than exclusive areas, while they seek opportunities to attempt extra-pair copulations. Black-faced Buntings live in the brushy and visually occluded habitats. These habitats would prevent males from performing mate guarding and territorial defence simultaneously. Males responded aggressively to extra-pair male intrusions which started and continued after pair formation and took part in incubation. Male-biased sex ratio in this area also makes males to give priority to mate guarding over territorial defence to assure their paternity.

Jpn J Ornithol 52: 13–23. 2003.

COMMENT

Management of the Great Cormorant-comments on Hayama (2002).

Masahiro FUJIOKA

Jpn J Ornithol 52: 24–28. 2003.

SHORT NOTES

Food item found in pellets of Long-eared Owls wintering in Ehime, Japan.

Satoshi KAWAGUCHI and Takahito YAMAMOTO

Sixty seven pellets of Long-eared Owls, *Asio otus*, were collected in a village, Ehime Prefecture, during 19 February 2001 to 6 April 2001. The bones of 164 *Mus musculus*, ten *Micromys minutus*, two *Apodemus speciosus*, two *Rattus* sp., seventeen *Pipistrellus abramus*, two *Myotis macrodactylus*, twelve *Crocidura dsinezumi* and a bird were found in the pellets. *M. minutus*, *P. abramus*, *M. macrodactylus* and *C. dsinezumi* were new records in diet of the Long-eared owls.

Jpn J Ornithol 52: 29–31. 2003.

Distribution of feeding sites of wintering Greater White-fronted Geese in Lake Izunuma-Uchinuma.

Tetsuo SHIMADA

Distribution of feeding sites of wintering Greater White-fronted Geese *Anser albifrons* around Lake Izunuma-Uchinuma (roost) was determined by direct observations during winter of 1997, 1998 and 1999. The 68.6% of 110 feeding flocks were observed in rice fields within 6 km from the lake.

Jpn J Ornithol 52: 32–34. 2003.

Effects of body mass on daily mass increment in Rhinoceros Auklet chicks receiving different amount of foods.

Tomohiro DEGUCHI and Tatsuhiko KAGAMI

Daily measurement of chick mass could be a useful method to estimate daily food intake under the assumption that the effects of the body mass on daily mass increment do not differ between chicks receiving different amount of food. To evaluate this assumption, 40 g and 60 g anchovy per day were fed to Rhinoceros Auklets chicks in semi-captivity. Negative relationships between chick mass and daily mass increment were found in 40 g- and 60 g-fed chicks. There was no significant difference in the slope of regression equation between 40 g-fed chicks (-0.037 ± 0.018) and 60 g-fed chicks (-0.041 ± 0.016). The intercept in 60 g fed chicks (17.578 ± 3.491 g) was larger than that in 40 g fed chicks (10.950 ± 3.491 g). Therefore, the daily amounts of food intake in Rhinoceros Auklet chicks can be estimated from body mass and daily mass increment.

Jpn J Ornithol 52: 35–38. 2003.

A parasitological survey of Hwamei *Garrulax canorus* and Red-billed Leiothrix *Leiothrix lutea* (Passeriforms: Terimiidae).

Tomoo YOSHINO, Kazuto KAWAKAMI, Hitoshi SASAKI, Kenji MIYAMOTO and Mitsuhiko ASAKAWA,

As one of ecological surveys of alien avian species in Japan, internal and external parasites of 4 individuals of Hwamei *Garrulax canorus* and 4 individuals of Red-billed Leiothrix *Leiothrix lutea* collected in Kanagawa, Tokyo, and Fukuoka Prefs., Japan during from July 1999 to November 2001, were investigated. *Ornithoica bistativa*, *Ornithomya avicularia* cf. *aobatoensis*, *Haemaphysalis flava* and *Centrorhynchus turdi* were obtained from Hwamei, and

Ornithonyssus sylvialum and *Anonchotaenia* sp, were obtained from the *Leiothrixes*, respectively. All of these external parasites and the acanthocephalan species are newly recorded from these two avian species in Japan.

Jpn J Ornithol 52: 39–42. 2003.

NUMBER 2

REVIEWS

Roles of behavioral science in conservation at the population level.

Go FUJITA

Application of recent advances in behavioral science is a growing subject in conservation biology. One possible reason for the growth of this approach is that behavioral scientists have become aware of the importance of conservation through their experience during field studies. In addition, there are three more plausible factors that can explain the approach. 1. As conservation biology has developed, both conservationists and behavioral scientists have recognized the importance of behavioral science in many cases of conservation activity. 2. Behavioral ecology has matured and many behavioral ecologists have shifted their interest to the application of their subject. 3. Studies of interactions between individual behavior and population dynamics have become active. Here, I briefly review model studies that have attempted to apply the behavioral sciences to conservation activities. The transfer and captive breeding of endangered populations often requires intensive conservation activity, such as the mating of individuals under conditions that differ from their natural habitats. Such activities require knowledge of the natural behavior and habits of the target species. Predicting the population dynamics of target animals is usually required to evaluate the effects of habitat change resulting from human disturbance on these populations. There are new approaches that incorporate behavioral processes into models of population dynamics. Certain models that include behavioral processes, foraging patch choice under game theory parameters, have succeeded in predicting population parameters such as winter mortality. Mating systems, sexual selection, regulation of the birth sex ratio and helping behavior are all suspected of affecting the effective population size of the target species. Helpers, in addition, can also serve to the function of absorbing the impacts of

environmental changes on the population.

Jpn J Ornithol 52: 71–78. 2004.

How can behavioral studies on individual animals contribute to wildlife conservation?

Masato MINAMI

The roles of behavioral studies of individuals in the conservation of wildlife, which should be important for the conservation of birds also, are briefly introduced and discussed in the light of two cases studies of the Asiatic Black Bear *Ursus thibetanus* and Sika Deer *Cervus nippon* in Japan. Some local populations of the bear, one of Japan's largest mammal species, are in danger of extinction. At Karuizawa town, Nagano Prefecture, central Japan, some bears have been visiting garbage disposal sites. Sixteen bears were captured, collared, and tracked using radio-telemetry, from July 1998 to September 2001. Three individuals were killed because they were staying within the town and judged as dangerous individuals. The other 16 bears were translocated. This individuals based management with radio-telemetry data can minimize risks of local population extinction of bears. On Kinkazan Island, Miyagi Prefecture, north-east Japan, most members of a 150-strong Sika Deer population were individually recognizable and have been tracked since 1989. Changes in body conditions, such as morphological and nutritional condition of individuals, and lifetime reproductive success were recorded. The data suggested that variances in lifetime reproductive successes among individuals were high, and the population dynamics can be strongly related to survival and reproductive success of the variation among individuals. This long-term study of the deer showed that reproductive strategies of individuals affected population dynamics. While, this study also showed that the population density, food availability, and stochastic variation in environment might seriously affect on survival and reproductive success of each individual.

Jpn J Ornithol 52: 79–87. 2004.

Behavioral approaches to agricultural damage and goose conservation.

Katsumi USHIYAMA, Tatsuya AMANO, Go FUJITA and Hiroyoshi HIGUCHI

Conflict between geese and agriculture has become a widely acknowledged problem in recent decades. Some of the goose species involved in such conflict are coincidentally considered to be of high conserva-

of interest. Behavioral ecology provides a useful framework for uniting agricultural damage management and conservation in a common scientific discipline. This paper summarizes the behavioral studies of habitat use by geese and their application in alleviating goose-agriculture conflicts. Behavioral approaches to habitat use by geese are useful in determining the underlying mechanism whereby damage occurs in a particular space and time, and enables efficient targeting and setting of management measures. Such management measures include the provision of alternative feeding areas combined with scaring devices, and habitat manipulation through the management of farming methods and human disturbance. From a broader perspective, understanding site selection by geese has important implications in guiding redistribution schemes, which is particularly important as the concentration of a population in a limited number of sites can have deleterious effects both on agriculture and on goose conservation. This behavioral knowledge can be integrated into a predictive model of goose distribution and population dynamics. Given evolutionary backgrounds, behavior-based models have the capability of predicting population level consequences of animals in response to habitat change. Such a model may serve as a cornerstone in predictive management and conservation.

Jpn J Ornithol 52: 88–96. 2004.

ARTICLES

Formation of foraging flocks using recruitment calls in Jungle Crows *Corvus macrorhynchos*.

Masayo SOMA and Toshikazu HASEGAWA

Recruitment calls are reported as one mechanism used by some birds and mammals for attracting conspecifics once an individual has found a food source, hence leading to the formation of foraging flocks/groups. Jungle Crows *Corvus macrorhynchos* sometimes give “kakaka” calls while foraging in flocks. We conducted field observations and playback experiments to examine whether these calls serve as recruitment calls leading to flock formation. Crows gave “kakaka” calls while foraging, and the size of foraging flocks was positively correlated with the number of calls given. Broadcasting “kakaka” calls attracted more Jungle Crows. There was also a positive correlation between pecking rates and the size of foraging flocks. The results indicate that “kakaka” calls are effective recruitment calls and that Jungle

Crows forage more efficiently in flocks.

Jpn J Ornithol 52: 97–106. 2004.

A Comparison of the feeding behavior of sympatric Varied Tit *Parus varius* and Great Tit *P. major*.

Akiko URATA and Keisuke UEDA

To study the food size preferences of Great *Parus major* and Varied tits *P. varius* we provided three sizes of sunflower seeds at a feeder at the forest edge on Mt Aburayama, Fukuoka, southern Japan. The Varied Tits preferred larger seeds than the Great Tits, and selected the size of seed that gave them greater feeding efficiency. The Great Tits carried larger seeds away from the feeder, whereas they ate smaller seeds immediately at the feeder. The Varied Tits always selected larger seeds at the feeder. It is suggested that the larger bill of the Varied Tit may affect this species difference in food size selection.

Jpn J Ornithol 52: 107–111. 2004.

SHORT NOTES

Partly albino fledglings in two Carrion Crow *Corvus corone orientalis* families.

Masaki KURO-O and Reiko KATAKURA

Four partly albino fledglings were observed in two Carrion Crow *Corvus corone orientalis* families in Hirosaki City, Aomori Prefecture, Japan, from 30 June to 9 August 2002. They all had white parts on the sub-terminal regions of the upper and under primary coverts, upper and under greater coverts, primaries, secondaries, and tertiaries. Two fledglings in one family had white in the subterminal regions of the rectrices as well as in the remiges. The latter two birds stayed with their parents for about 20 days longer than their single normally plumaged sibling.

Jpn J Ornithol 52: 112–115. 2004.

The parasitic helminths of avian species in Niigata Prefecture, Japan.

Shigeru NAKAMURA, Tomoo YOSHINO, Jun SATO, Akira CHIBA and Mitsuhiro ASAKAWA

As part of ongoing research into the conservation of wild avian species in Niigata Prefecture, helminthological examination was conducted between March and November 2002 in Niigata Prefectural Bird Protection Center, Japan. A total of 50 individuals of 28 avian species was investigated, with parasitic

helminthes collected from 26 individuals. The parasitic helminths belonged to 13 nematode, two acanthocephalan, and three trematode genera, and unidentified cestodes were also collected. Three genera, *Epo-*
midostomum (host: *Anser albifrons*), *Viktorocara* (host: *Fulmarus glacialis*) and *Diomedeenema* (host: *Ardea cinerea*) were new locality records in Japan.

Jpn J Ornithol 52: 116–118. 2004.

OBSERVATIONAL DATA

The capture record of Taczanowski's Grasshopper Warblers *Locustella pleskei* at the Hososhima, Miyazaki Prefecture.

Yasuhiro YAMAGUCHI, Hiroshi KIKUCHI, Tetsuro KAMETANI, Kyoko YAMAGUCHI and Shinichirou

UENO

Jpn J Ornithol 52: 119–121. 2004.

Record of Dovekie *Alle alle* in Japan.

Yutaka NAKAMURA, Yutaka TAKANOHASHI, Akira ASO, Toshiko TAKANOHASHI, Naomi SYUTO, Sayuri SATO and Isako SHIOMOKAWA.

Jpn J Ornithol 52: 122–123. 2004.

A record of Ferruginous Duck *Aythya nyroca* in Yonago Warterbirds Sanctuary, Tottori Prefecture.

Keisuke KIRIHARA

Jpn J Ornithol 52: 124–125. 2004.

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Mori et al. (1997) or (Mori et al. 1997; Richard et al. 1999a)

Journals:

Yamaguchi N & Kawano KK (2001) Effect of body size on the resource holding potential of male varied tits *Parus varius*. *Jpn J Ornithol* 50: 65–70.

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ORNITHOLOGICAL SCIENCE

Volume 3 Number 1 January 2004

Contents

SPECIAL FEATURE

Invasive bird species

Sodhi NS & Eguchi K

Introduction 1

Eguchi K & Amano HE

Spread of exotic birds in Japan 3

Kawakami K & Yamaguchi Y

The spread of the introduced Melodious
Laughing Thrush *Garrulax canorus* in Japan 13

Tojo H & Nakamura S

Breeding density of exotic Red-billed
Leiothrix and native bird species on Mt.
Tsukuba, central Japan 23

Brook BW

Australasian bird invasions: accidents of
history? 33

Leven MR & Corlett RT

Invasive birds in Hong Kong, China 43

Yap CAM & Sodhi NS

Southeast Asian invasive birds: ecology,
impact and management 57

ORIGINAL ARTICLES

Nakamura M & Murayama S

Are Carrion Crows that congregate in spring
roosts juveniles or adults? 69

**Paszkowski CA, Sodhi NS, Jamieson S &
Zohar SA**

Habitat use and foraging behavior of male
Black-and-white Warblers (*Mniotilta varia*) in
forest fragments and in a contiguous boreal
forest 75

**Yamazaki Y, Yamada H, Murofushi M,
Momose H & Okanoya K**

Estimation of hearing range in raptors using
unconditioned responses 85

A List of Referees 2003 93

**Abstracts of the Japanese Journal of
Ornithology, Volume 52 93**

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Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand

Pilai POONSWAD^{1,*}, Atsuo TSUJI² and Narong JIRAWATKAVI¹

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Abstract Hornbills are omnivorous and the breeding male delivers all food required by the nest-confined female and chicks. The contributions of different food types, in terms of breeding nutrition, have not previously been documented. In Khao Yai National Park, Thailand, we sampled the identity and number of food items delivered daily to the nest, during each week of the nesting cycle, by two small and two large sympatric species of hornbills. We then recorded the mass and estimated the nutrient content of each food type from analyses of protein, fat, carbohydrate, calcium, and energy. The overall pattern of nutrient delivery during the nesting cycle was the same for each of the four hornbill species, and was related to sequential demands for egg, feather, and chick development. The two larger species delivered mainly carbohydrates (Great *Buceros bicornis* 50%, Wreathed *Aceros undulatus* 57%) and less fat and protein. The smallest, Oriental Pied Hornbill *Anthracoceros albirostris*, also delivered mostly carbohydrate (45%), but the small White-throated Brown Hornbill *Anorrhinus austeni* delivered equivalent proportions of protein (32%), fat (30%), and carbohydrate (37%). Comparison of the incubation and nestling phases showed that more protein was delivered during the nestling phase for all species, except for Great Hornbill where the compression of egg production, incubation, and molt had to be completed by midway through the nestling phase and so high levels of fat and protein were delivered during incubation. We confirmed that fruits are an important source of all nutrients, especially fat, for all four hornbill species, but suggest that delivery of animal protein may be linked, in some way, to breeding success. Oriental Pied Hornbill broods, that received protein at about 1.05% of brood mass per day, had the highest breeding success (96%) whereas Wreathed Hornbills received only 0.57% protein and had only 67% success, while the other two species delivered intermediate amounts of protein and had intermediate breeding success.

Key words Breeding nutrition, Frugivore, Hornbill, Nesting diet, Omnivore, Thailand

Breeding hornbills, like many other birds, must collect sufficient food to satisfy both their own nutritional requirements and those of any offspring they raise. In hornbills, provision of these nutrients is the responsibility of the male because the female seals herself into the nest and is fed by the male throughout the egg-laying, incubation and, with the chick(s), the nestling phase (Kemp 1995). In most hornbill species, the breeding female, after a phase of courtship feeding by the male, seals herself into the

nest cavity about a week before egg-laying and, once laying commences, starts her annual molt of rectrices and remiges, further increasing the nutritional demand imposed on the male (Poonswad 1993; Kemp 1995).

There is some variation between hornbill species in the timing of the female's emergence or whether assistance is available to the male from members of a group. Species also differ in size, duration of the nesting cycle and number of eggs laid and chicks raised (Poonswad et al. 1987; Kemp 1995), all of which influence the nutrient requirements of nest inmates. Food delivered to the nest also varies between

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species, habitats, seasons and phases of the nesting cycle. It may depend in part on availability, but also on nutrient demands, such as calcium for egg or skeleton formation, or particular amino acids for feather growth.

The diets of many bird species are predominately either frugivorous or carnivorous during breeding, but in omnivores, such as forest hornbills, both food types occur regularly in the diet (Poonswad et al. 1987; Kemp 1995). The proportion of nutrients contributed by different food types at different phases of the nesting cycle has not previously been recorded for hornbills. Four species of hornbills breed in Khao Yai National Park, central Thailand, two large species, Great Hornbill *Buceros bicornis* and Wreathed Hornbill *Aceros undulatus*, and two smaller species, White-throated Brown Hornbill *Anorrhinus austeni* and Oriental Pied Hornbill *Anthracoceros albirostris*. Their dietary choices have been reported (Poonswad et al. 1987, 1998), as have differences in their size, nesting cycle and breeding biology (Poonswad 1993; Table 1). Here, we concentrate on intra-specific patterns and sources of nutrients delivered to nest inmates during the incubation and nestling phases of the nesting cycle, based on the identity and analysis of food items delivered to the nest inmates; an attempt at inter-specific comparisons is also presented.

METHODS

We conducted this study in the 70 km² Khao of Yai National Park (ca. 14°15–30'N, 101°20–24'E), Thailand, an area of tall monsoon forest (62 km²) with patches of open grassland (8 km²; Poonswad et al. 1998). We observed hornbill nests during the breeding seasons (January–June) of 1982–1985 and recorded all food items delivered (0700–1700) to the nesting female and/or chicks by the breeding male and any other helpers. We observed each hornbill species at 2–10 day intervals, to provide weekly samples of full-day observations that covered the whole nesting cycle (Table 2). Breeding success, i.e. the number of chicks fledging per nest, was also recorded.

We observed food items delivered to the nest using binoculars (8×30), a spotting scope (×20 and ×40), or took photographs (using 400–800 mm telephoto lenses), depending on the distance from the nest. We identified items as fruit or animal and classified them by direct observation, by collection of debris below

Table 1. Attributes of size and breeding biology for four species of hornbills that breed in Khao Yai National Park, Thailand (from Poonswad 1993 unpublished data; Kemp 1995, 2001).

Hornbill species	Median female mass (g)	Nesting cycle, weeks (incubation/nesting) (ratios)	Clutch size, range (mean)	Mean brood size, (range, sample)	Female + mean brood mass, g (ratios)	Egg volume (cc)	Exceptional breeding biology
Great	2,211	20 (7/13) (1.4)	1–4	1 (0, N=66)	3,316 (2.1)	71	Female emerges 6 weeks after chicks hatch
Wreathed	1,950	20 (7/13) (1.4)	1–3	1 (0, N=27)	3,900 (2.5)	60	
White-throated Brown	755	15 (5/10) (1.1)	1–5	2.6 (1–4, N=15)	2,718 (1.7)	29	Cooperative group, 1–5 helpers for male at nest
Oriental Pied	624	14 (5/9) (1.0)	1–3	1.5 (1–2, N=12)	1,560 (1.0)	29	

Table 2. Sample sizes for observations at nests of four sympatric species of hornbills in Khao Yai National Park, Thailand. Incubation and nestling phases were determined from direct observation or published information, and the incubation phase was assumed to include the pre-laying interval of one week (Poonswad 1993; Kemp 1995).

Hornbill species	No. of pair-years	Total no. of days of observation	No. of full-day observations, mean days/week and phase duration					
			Incubation phase			Nestling phase		
			Full-days	Days/week	Phase duration	Full-days	Days/week	Phase duration
Great	16	437	78	11.1	Weeks 1–7	119	9.2	Weeks 8–20
Wreathed	9	227	35	5.0	Weeks 1–7	63	4.8	Weeks 8–20
White-throated	14	258	46	9.2	Weeks 1–5	92	9.2	Weeks 6–15
Brown								
Oriental Pied	24	449	62	12.4	Weeks 1–5	157	17.4	Weeks 6–14

the nest, or by comparison with specimens collected nearby. Some plant samples were sent for further identification to the Forest Herbarium, Royal Forest Department, Bangkok, Thailand.

Using an average weight for each food item, we estimated the total wet weight consumed for each item per day. Average weights of fruits were obtained from samples dropped below nests or collected later from fruiting trees. Average weights of animals were obtained from fresh specimens dropped below nests or from specimens of similar size caught elsewhere in the study area (of the same group but not always of the same species, due to the difficulty of collecting and identifying most small animals in tropical forest).

We also determined nutritional values in g/wet weight (protein, fat, carbohydrate (CHO), calcium, and energy content) for each type of food. Fruits were analyzed by the Food Analysis Laboratory, Institute of Nutrition, Mahidol University at Salaya, Nakhon Pathom, Thailand. A few animal food items were also sent there for analysis, but most values for animal foods were obtained from published sources (Department of Health 1978, 1984; Puwastien & Sungpuag 1983). Samples of specific animals were difficult to obtain from the forest, so, where necessary, data for animals of the same genus or family as those identified as hornbill food items were substituted in the analyses.

Food samples were weighed, to obtain the wet weight in grams, blended with an ordinary mixer; then frozen for 24 hours before being transferred into a freeze drier, if the sample was to be analyzed later. Nutritional values, including protein, fat, and calcium were determined by Kjeldahl AOAC 981.10, Soxhlet AOAC 945.16, and atomic absorption AOAC 975.03, respectively. Carbohydrate was obtained by subtract-

ing the sum of moisture (drying AOAC 925.45), protein, fat, and ash (dry ashing) from 100. Energy was calculated using the general factors of 16.7, 37.5, and 16.7 kJ/g from protein, fat, and carbohydrate, respectively.

A comparison of the quantities of food and nutrients delivered to nest inmates among these four hornbill species, involves correcting for differences in female body mass, clutch and brood sizes, and the length of nesting cycle and its phases (Table 1). Therefore, although mean daily delivery rates of food types and nutrients are compared within species as absolute amounts, useful for ecological comparisons, biological comparison requires some sort of correction for inter-specific differences. In an attempt at correction, ratios were calculated between values for each species by taking the species with the lowest values, the smallest Oriental Pied Hornbill (Table 1), as one unit. The mean values for each species were then adjusted using either ratios of the mean mass of nest inmates or ratios of the duration of the total nesting cycle. The mean mass of nest inmates for each species was calculated as the sum of the median female mass plus the mean brood size multiplied by the median female mass, except for Great Hornbill where the female leaves the nest early in the nestling phase and is scored for only half of her mass contribution (Table 1). Chick mass at different ages and growth curves were unavailable for any of the hornbill species, so the mass of the adult female, less than the adult male, was substituted for the mass of a chick at fledging. Any excess of the adult female mass over the real fledgling mass would offset any additional nutritional requirements of chicks during their development.

Statistical analyses were performed with SigmaSta

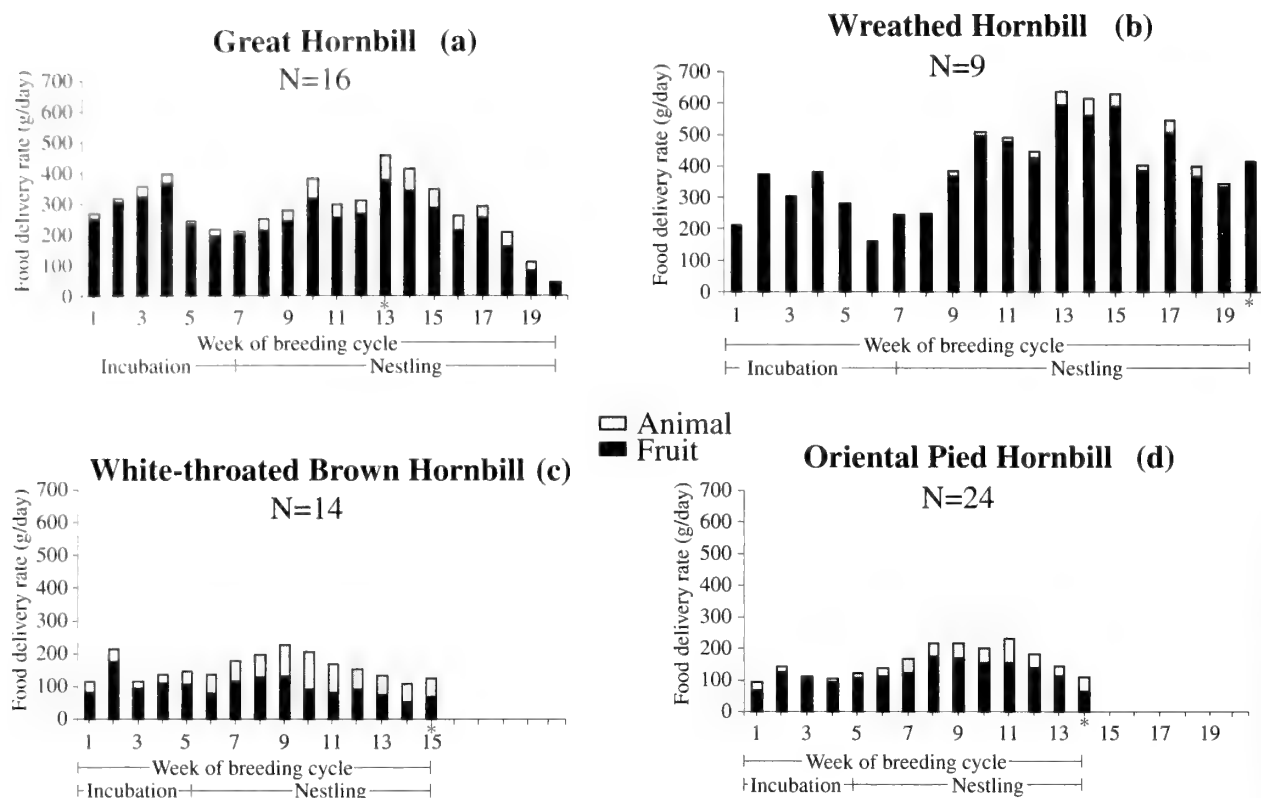


Fig. 1. Quantity of food (estimated g/day) and proportion as fruits and animals delivered by wet weight to the nest inmates of four hornbill species: Great Hornbill (a), Wreathed (b), White-throated (c), and Oriental Pied (d) in Khao Yai National Park, Thailand, at weekly intervals during the nesting cycle. * time of female emergence.

2.0 (Jardel Corporation 1995) We used Mann-Whitney Rank Sum Test (T, for medians) for intra-specific comparisons of each phase of the nesting cycle and the Kruskal-Wallis ANOVA (F, for means) or One Way ANOVA on Ranks (H, for medians) for All Pair-wise Multiple Comparison Procedures (Dunn's Method, for significance at $P < 0.05$) of inter-specific values.

RESULTS

1) Intra-specific patterns of food delivery by mass and food type during the incubation and nestling phases

The weekly pattern of food delivery over the whole nesting cycle was similar for each hornbill species (Fig. 1), taking into account the differences in the lengths of their nesting cycles (Table 1). There were two main peaks, the first during early incubation and the second midway through the nestling phase, even though the quantities and proportions of fruits and animals in the diet varied between species.

Great Hornbill food delivery rose to a peak

halfway through the incubation phase (Week 4) and nestling phase (Week 13, also the time of the female's emergence) but then dropped off markedly until fledging (Fig. 1a). Only the delivery of animal food was significantly higher after hatching ($T = 5121.5$, $N_1 = 78$, $N_2 = 119$, $P < 0.001$), whereas fruit delivery showed no significant change between the incubation and nestling phases. The female Great Hornbill would have consumed all animal food delivered during incubation, but once she emerged from the nest, all animal food would have become available to the chick.

Wreathed Hornbill food delivery also showed a low peak midway through incubation (Weeks 2–4), a drop before hatching, but then a high and sustained feeding rate throughout the nestling phase with a peak in Weeks 13–15, all of it supplied by the male alone to the female and a single chick (Fig. 1b). The incubating female received little animal food, but there was a significant increase in animals and fruits once the chick had hatched ($T = 913.0$, $N_1 = 35$, $N_2 = 63$, $P < 0.001$ and $T = 1322.0$, $N_1 = 35$, $N_2 = 63$, $P = 0.002$, respectively), the increase in animals suffi-

ciently obvious to confirm hatching.

White-throated Brown Hornbill food delivery by the male and nest helpers appeared to increase markedly during egg-laying (Week 2), especially for fruits (Fig. 1c), although there was no significant difference in the rates of fruit delivery before and after hatching. Food delivery peaked again midway through the nestling phase (Week 9), probably through the significantly higher delivery rate to the

female and several chicks of animal foods after hatching ($T=2126.0$, $N_1=46$, $N_2=92$, $P<0.001$), and then declined towards fledging.

Oriental Pied Hornbill food delivery also peaked during egg-laying (Week 2) and then, after hatching, rose steadily to an extended peak midway through the nestling phase (Weeks 8–11) before declining towards fledging (Fig. 1d). The Oriental Pied Hornbill delivered significantly more fruit and animal foods

Table 3. Statistical comparison of daily rates (range, mean, SD, median) of protein, fat, carbohydrate, calcium, and energy delivered to nest inmates by wet weight during the incubation and nestling phases for four sympatric species of hornbills in Khao Yai National Park, Thailand. GH=Great Hornbill, WH=Wreathed Hornbill, BH=White-throated Brown Hornbill, PH=Oriental Pied Hornbill.

	<i>Incubation phase</i>				<i>Nestling phase</i>			
	GH	WH	BH	PH	GH	WH	BH	PH
N (weeks)	7	7	5	5	13	13	10	9
Protein (g/day)								
Range	6.1–23.8	3.2–9.0	6.1–11.3	4.7–6.5	1.8–28.3	7.2–25.7	9.8–22.0	5.7–15.1
Mean	11.0	6.5	8.6	5.5	17.2	15.6	14.5	10.9
SD	6.1	2.3	2.5	0.7	7.8	5.6	4.1	3.1
Median	9.5	6.4	7.9	5.3	16.3	15.6	13.6	10.5
					$T=48.5$	$T=31.0$	$T=19.0$	$T=17.00$
					$P=0.05$	$P<0.001$	$P=0.01$	$P=0.008$
Fat (g/day)								
Range	6.5–56.1	4.5–35.2	7.2–11.6	6.0–9.2	1.7–14.9	8.9–61.6	8.6–17.9	7.4–14.0
Mean	19.7	19.7	9.6	7.5	11.3	21.6	12.1	10.8
SD	16.4	11.2	1.7	1.2	3.5	14.3	2.7	2.1
Median	15.2	18.8	10.2	7.3	12.3	20.0	12.1	10.9
					$T=100.00$	$T=73.0$	$T=25.0$	$T=18.0$
					$P=0.04$	$P=1.0$	$P=0.08$	$P=0.01$
Carbohydrate (g/day)								
Range	20.7–61.0	15.5–43.0	11.1–19.3	7.7–19.2	5.9–39.2	37.3–79.3	7.1–19.0	4.4–22.9
Mean	32.6	30.1	13.8	13.3	26.3	53.2	13.3	15.5
SD	13.9	10.7	3.3	4.1	10.1	14.1	3.8	6.0
Median	26.3	30.6	12.5	13.1	26.9	49.5	13.4	16.9
					$T=78.0$	$T=36.0$	$T=40.5$	$T=29.0$
					$P=0.75$	$P=0.003$	$P=1.0$	$P=0.29$
Calcium (g/day)								
Range	0.39–1.95	0.49–0.90	0.27–0.78	0.30–0.42	0.02–2.74	0.82–2.21	0.40–1.22	0.51–1.05
Mean	1.13	0.72	0.48	0.36	1.43	1.37	0.73	0.74
SD	0.56	0.13	0.25	0.06	0.77	0.45	0.26	0.18
Median	0.85	0.72	0.31	0.40	1.3	1.4	0.67	0.76
					$T=61.0$	$T=29.00$	$T=28.0$	$T=15.0$
					$P=0.34$	$P<0.001$	$P=0.16$	$P=0.003$
Energy (kJ/day)								
Range	706–3,520	481–2,187	572–894	485–754	192–1,652	1,186–3,945	605–1,334	620–1,067
Mean	1,469	1,353	735	596	1,150	1,959	917	845
SD	937	625	137	99	401	789	210	156
Median	1,131	1,323	711	593	1,111	1,764	889	851
					$T=77.0$	$T=55.0$	$T=26.0$	$T=17.0$
					$P=0.81$	$P=0.15$	$P=0.10$	$P=0.008$

Table 4. Mean daily rates (from Table 2) and proportions of energy-producing protein, fat, and carbohydrate delivered to nest inmates by wet weight during the incubation and nestling phases for four sympatric species of hornbills in Khao Yai National Park, Thailand. * % of nutrients delivered, not including crude ash, present in the actual food remains.

Hornbill species	Protein		Fat		Carbohydrate		Total	
	g/day	%	g/day	%	g/day	%	g/day	%*
Incubation phase								
Great	11.0±6.1	17.4	19.7±16.4	31.1	32.6±13.9	51.5	63.3	100
Wreathed	6.5±2.3	11.5	19.7±11.1	35.0	30.1±10.7	53.5	56.3	100
White-throated Brown	8.6±2.5	26.9	9.6±1.7	30.0	13.8±3.3	43.1	32.0	100
Oriental Pied	5.5±0.7	20.9	7.5±1.2	28.5	13.3±4.1	50.6	26.3	100
Nestling phase								
Great	17.2±7.8	31.4	11.3±3.5	20.6	26.3±10.0	48.0	54.8	100
Wreathed	15.6±5.6	17.3	21.6±14.3	23.9	53.2±14.1	58.8	90.4	100
White-throated Brown	14.5±4.1	36.3	12.1±2.7	30.3	13.3±3.8	33.3	39.9	100
Oriental Pied	10.9±3.1	29.3	10.8±2.1	29.0	15.5±6.0	41.7	37.2	100
Total								
Great	28.2	23.9	31.0	26.2	58.9	49.9	118.1	100
Wreathed	22.1	15.1	41.3	28.2	83.3	56.7	146.7	100
White-throated Brown	23.1	32.1	21.7	30.2	27.1	36.7	71.9	100
Oriental Pied	16.4	25.8	18.3	28.8	28.8	45.4	63.5	100

during the nestling phase than the incubation phase ($T=4394.5$, $N_1=57$, $N_2=142$, $P<0.001$ and $T=4319.5$, $N_1=62$, $N_2=157$, $P<0.001$, respectively), to the female and several chicks.

2) Intra-specific patterns of nutrient delivery during the incubation and nestling phases

The estimated weekly pattern of nutrients delivered to nest inmates over the whole nesting cycle varied considerably by nutrient type and hornbill species (Tables 3 & 4, Figs. 2–5).

Great Hornbill nutrient delivery comprised similar proportions overall of protein (23.9%) and fat (26.2%) but more carbohydrate (49.9%) (Table 4). Significantly more fat was delivered during incubation than the nestling phase (Table 3), possibly an anomaly due to a peak soon after egg-laying (Week 3, Fig. 2b). There were no significant differences for other nutrients, including energy (Table 3), even though all other nutrients also appeared to peak in Week 3 (except for calcium, Fig. 2d) and the delivery rates for protein, calcium and to a less extent carbohydrate rose again midway through the nestling phase (Fig. 2a, d, and c). The peak in Week 3 of fat derived mainly from lipid-rich fruits, the peak of protein derived from similar quantities of fruit and animal foods and the peak of carbohydrate from fruit (Fig. 2b, a, and c respectively).

Wreathed Hornbill nutrient delivery was low over-

all in protein (15.1%), medium in fat (28.2%) and high in carbohydrate content (56.7%) (Table 4). Mean delivery rates of protein, carbohydrate, and calcium were significantly higher during the nestling phase (Table 3, Fig. 3a, c, and d), and although apparently also higher for fat and energy these were not significant.

White-throated Brown Hornbill nutrient delivery yielded similar proportions overall of protein (32.1%), fat (30.2%), and carbohydrate (36.7%) (Table 4). Only protein increased significantly during the nestling phase (Table 3, Fig. 4a), although other nutrients also appeared to increase during the same phase (Fig. 4).

Oriental Pied Hornbill nutrient delivery yielded similar proportions overall of protein (25.8%) and fat (28.8%) but higher carbohydrate (45.4%) (Table 4). There were significant increases during the nestling phase for all nutrients (protein, fat, energy, and calcium) except carbohydrate (Table 3, Fig. 5).

3) Intra-specific patterns of nutrient delivery by food type

Fruit and animal foods contributed to all nutrient classes measured in this study. However, the proportions of these foods delivered to nest inmates and the quantities of their contributions to the main nutrient classes, varied among hornbill species (Figs. 2–5).

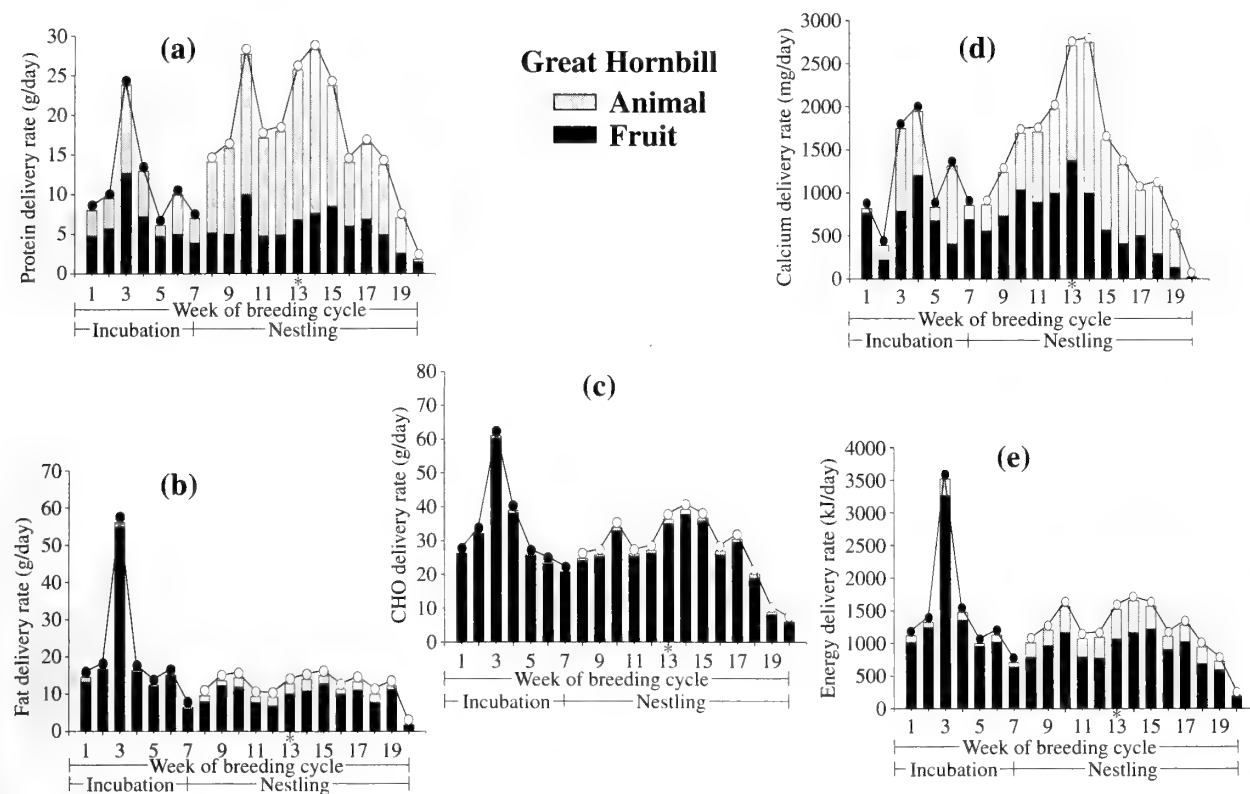


Fig. 2. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of Great Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

Protein

Both fruits and animals were important protein sources for nesting Great Hornbill (Fig. 2a) and their delivery rates did not significantly differ. In contrast, fruits were the major source of protein in the diet of the Wreathed Hornbill, with a significantly higher delivery rate than for animals ($T=586.0$, $N_1=20$, $N_2=20$, $P<0.001$; Fig. 3a), both before and after hatching ($T=77.0$, $N_1=7$, $N_2=7$, $P=0.002$ and $T=250.5$, $N_1=13$, $N_2=13$, $P<0.001$, respectively).

Animal food was the major source of protein in the diet of White-throated Brown and Oriental Pied Hornbills, since delivery rates from fruits were significantly lower ($T=121.0$, $N_1=15$, $N_2=15$, $P<0.001$ and $T=152.0$, $N_1=14$, $N_2=14$, $P=0.02$, respectively; Figs. 4a and 5a).

Fat

The main source of fat delivered by all four hornbill species was lipid-rich fruits, as shown by the significantly higher delivery rate for fruits than animals (Great Hornbill $T=602.5$, $N_1=20$, $N_2=20$, $P<0.001$;

Wreathed Hornbill $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; White-throated Brown Hornbill $T=345.0$, $N_1=15$, $N_2=15$, $P<0.001$; Oriental Pied Hornbill: $T=301.0$, $N_1=14$, $N_2=14$, $P<0.001$; Figs. 2b, 3b, 4b, and 5b). This was especially evident for the two larger species, Great and the Wreathed Hornbills, where the delivery rate of fat from fruits was 8.9 times and 25.2 times higher respectively than from animals (Figs. 2b and 3b). Delivery rates of fats from fruits and animals were both higher after than before hatching for Great Hornbill ($T=77.0$, $N_1=7$, $N_2=7$, $P<0.001$ and $T=252.5$, $N_1=13$, $N_2=13$, $P<0.001$, respectively).

Carbohydrate

Fruits were the main source of carbohydrate for all four species (Figs. 2c, 3c, 4c, and 5c), with a significantly higher delivery rate than from animals (Great Hornbill $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; Wreathed Hornbill $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; White-throated Brown Hornbill $T=345.0$, $N_1=15$, $N_2=15$, $P<0.001$; Oriental Pied Hornbill

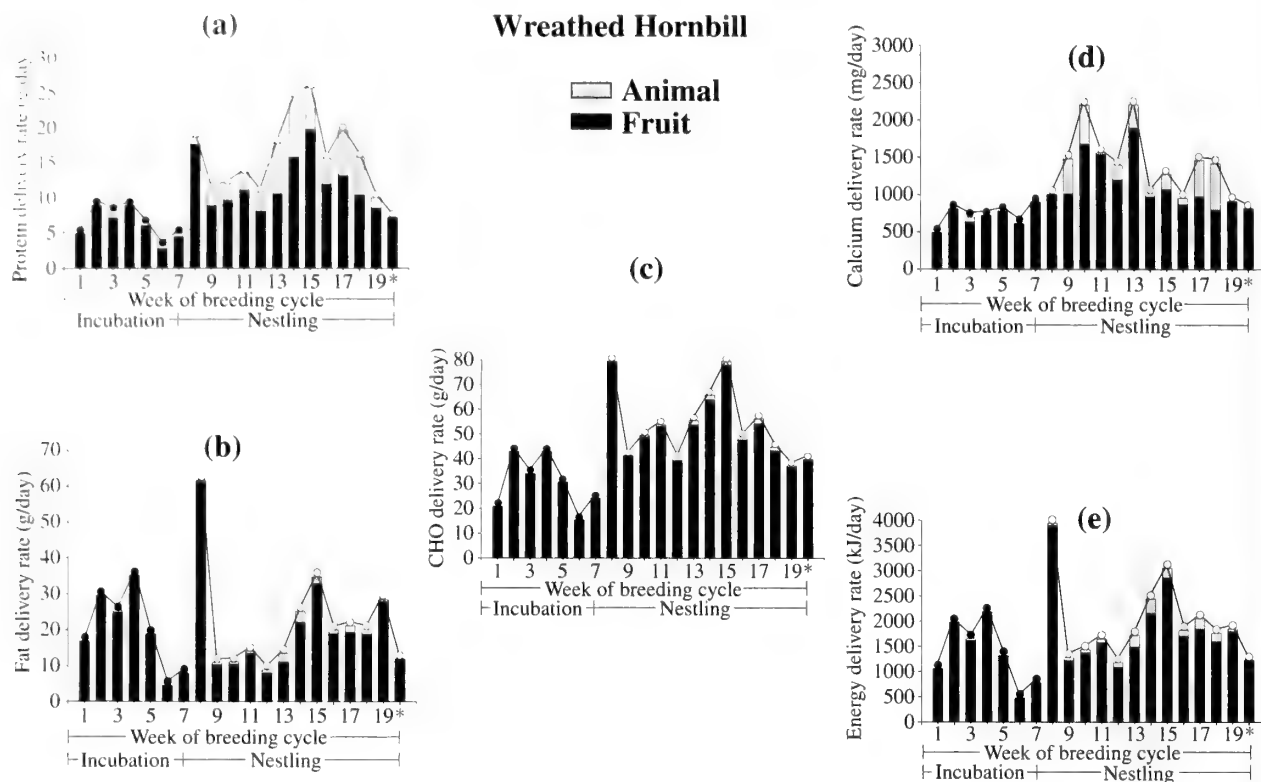


Fig. 3. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of Wreathed Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

$T=299.0$, $N_1=14$, $N_2=14$, $P<0.001$, and this difference occurred both before and after hatching for Wreathed Hornbill ($T=77.0$, $N_1=7$, $N_2=7$, $P<0.001$ and $T=260.0$, $N_1=13$, $N_2=13$, $P<0.001$, respectively).

Calcium

The main source of calcium depended on hornbill species (Figs. 2d, 3d, 4d and 5d). Wreathed Hornbill acquired significantly more calcium from fruits than from animals ($T=607.0$, $N_1=20$, $N_2=20$, $P<0.001$; Fig. 3d), whereas White-throated Brown Hornbill acquired most calcium from animals ($T=167.5$, $N_1=15$, $N_2=15$, $P=0.008$; Fig. 4d). Both Great and Oriental Pied Hornbills acquired calcium about equally from fruits and animals, with no significant differences (Figs. 2d and 5d). Delivery rates of calcium from fruits were higher both before and after hatching for Wreathed Hornbill ($T=77.0$, $N_1=7$, $N_2=7$, $P<0.001$ and $T=260.0$, $N_1=13$, $N_2=13$, $P<0.001$, respectively; Fig. 3d).

Energy

Energy can be derived from proteins, fats, carbohydrates or a combination of these nutrients in fruits and animal foods. Fruits were the main overall source of energy and were delivered significantly more than animals by all four species (Great Hornbill, $T=598.0$, $N_1=20$, $N_2=20$, $P<0.001$; Wreathed Hornbill, $T=610.0$, $N_1=20$, $N_2=20$, $P<0.001$; White-throated Brown Hornbill, $T=330.0$, $N_1=15$, $N_2=15$, $P<0.001$; Oriental Pied Hornbill, $T=300.0$, $N_1=14$, $N_2=14$, $P<0.001$), particularly the Wreathed Hornbill (Figs. 2e, 3e, 4e, and 5e). However, energy delivery from animals significantly increased for all species after hatching, Great ($T=249.0$, $N_1=13$, $N_2=13$, $P<0.001$), Wreathed ($T=260.0$, $N_1=13$, $N_2=13$, $P<0.001$), White-throated Brown ($T=144.0$, $N_1=10$, $N_2=10$, $P=0.004$), and Oriental Pied Hornbills ($T=126.0$, $N_1=9$, $N_2=9$, $P<0.001$) (Figs. 2e, 3e, 4e, and 5e).

For Great and Wreathed Hornbills, fat and carbohydrate were equally important sources of energy by mass, although not necessarily by calorific value per

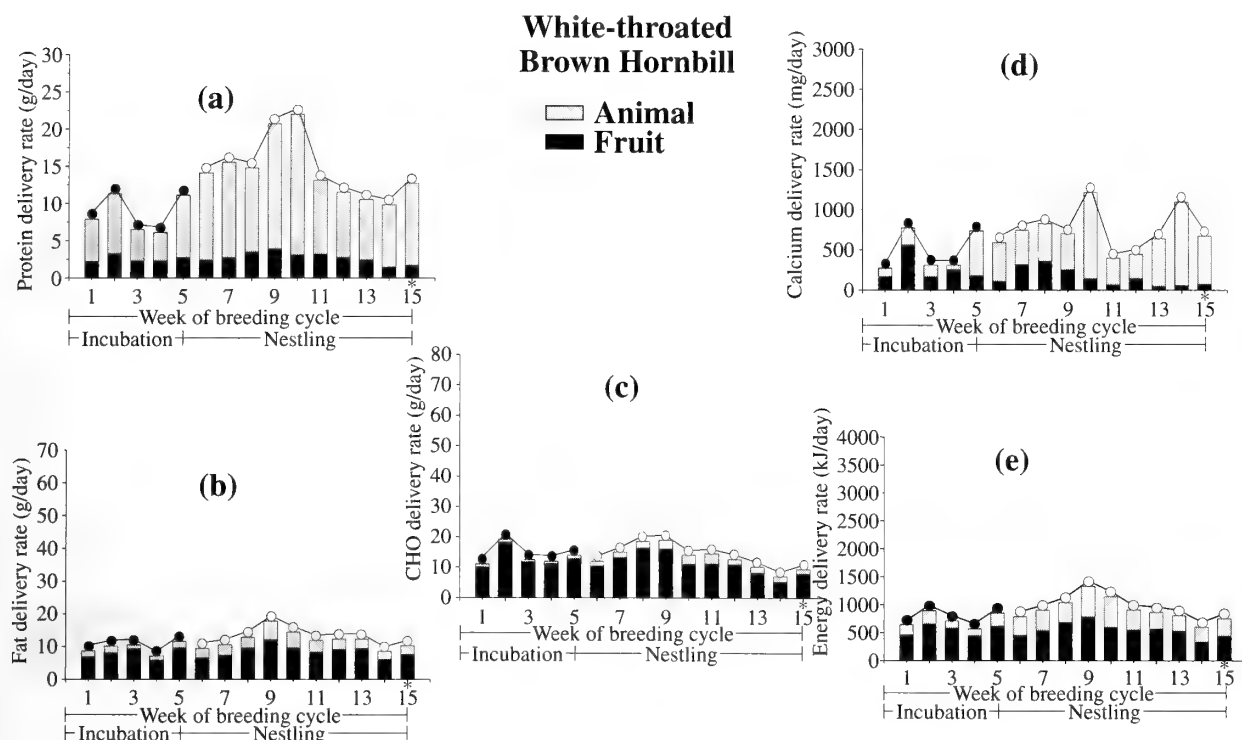


Fig. 4. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of White-throated Brown Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

unit weight. Mean delivery rates of both nutrition classes were significantly higher than the delivery rate of protein ($H=19.5$, $df=2$, $P<0.001$ and $H=33.7$, $df=2$, $P<0.001$, respectively; Table 4). For the White-throated Brown and Oriental Pied Hornbills, fat was the major source of energy ($F=33.8$, $df=2$, $P<0.001$ and $F=23.7$, $df=2$, $P<0.001$, respectively).

4) Inter-specific comparisons of patterns of nutrient delivery

Comparisons between species of the quantities of food and nutrients delivered to nest inmates is complicated by inter-specific differences in body, clutch and brood sizes, and in the duration of the nesting cycle and its phases (Table 1). Results of the calibrated means are shown for each of the nutrients (Table 5) and for the quantities of nutrients and total energy (Table 6) even though protein and energy requirements are proportional to body-mass^{0.75} (Kleiber's rule; Kleiber 1961). No statistical test of any differences between species was considered appropriate, but adjustment of the means did reduce

variance between the species (cf. Table 3), suggesting more equivalent comparisons.

Protein delivery rates adjusted for brood mass for all species were similar to that of the Oriental Pied Hornbill during the incubation phase, except for being lower for the Wreathed Hornbill (Table 5). During the nestling phase, adjusted delivery rates were higher than during the incubation phase for all species, especially the Oriental Pied Hornbill. Adjusted fat delivery rates were low during incubation for White-throated Brown Hornbill and high for Great Hornbill, but were highest for nestling Oriental Pied Hornbill and lowest for Great Hornbill (Table 5). Adjusted carbohydrate delivery rates were most varied among species, lowest for White-throated Brown Hornbill during both incubation and nestling phases, but highest for incubating Great Hornbill and nestling Wreathed Hornbill (Table 5). Adjusted calcium delivery rates were lower during the incubation than the nestling phase for all species, but with the greatest increase for nestlings of Oriental Pied Hornbill (Table 5). Adjusted energy delivery rates to the female during incubation were lowest for White-

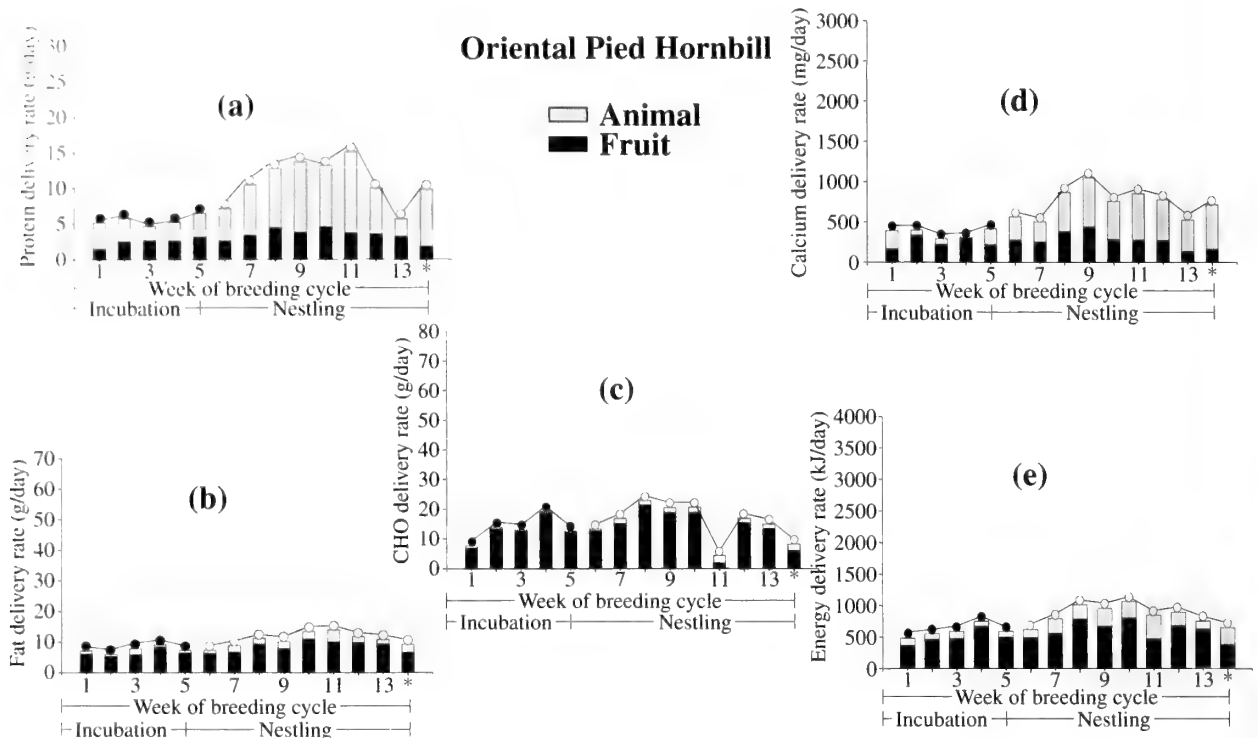


Fig. 5. Estimated mean daily delivery rates of nutrients derived from fruit and animal food by wet weight, including protein (a), fat (b), carbohydrate (c), calcium (d) and energy (e) to nest inmates of Oriental Pied Hornbill and a total of nutrient delivery daily during each week of the incubation (solid circles) and nestling (open circles) phases. * time of female emergence.

throated Brown Hornbill, but rose during the nestling phase for all species except Great Hornbill where the incubating female received more energy than the nestling (Table 5).

Delivery rates for nutrients and total energy, once adjusted for the duration of the nesting cycle, reduced considerably the overall differences between species (Table 5 cf. Table 4). Adjusted protein delivery rates were especially important to Great and White-throated Brown Hornbills, and more important in the nestling than the incubation phases for all species. Adjusted fat delivery rates were important during incubation for the larger species, Great and Wreathed Hornbills, but especially during the nestling phase for the smaller species-pair of White-throated Brown and Oriental Pied Hornbills, although about equal in both phases for Wreathed Hornbill. Adjusted carbohydrate delivery rates were especially important to both larger species during incubation, particularly for Great Hornbill, and markedly increased during the nestling phase for Wreathed Hornbill, but varied least in both phases for the smaller species. Adjusted delivery rates for total energy were only highest during

the incubation phase for Great Hornbill, being similar and higher during the nestling phase for all the other species, particularly for Wreathed Hornbill.

The percentages of nutrients delivered to the nestlings also needs to be adjusted by the brood mass (Table 6), especially for any comparisons with fledging success. The adjusted percentages of nutrients and energy for the Oriental Pied Hornbill were 1.05 for protein, 1.17 for fat, 1.85 for carbohydrate, and 92.38 for energy (Table 6) while the other three species had relatively lower protein intakes, especially the Wreathed Hornbill during the incubation phase (Table 3). The Oriental Pied Hornbill had the highest breeding success (95.8%) and the Wreathed Hornbill the lowest (66.7%, Table 6).

DISCUSSION

1) Food delivery pattern

The overall pattern of food delivery to nest inmates was similar for all four hornbill species, despite differences in size, duration of nesting cycle and breeding strategy. There was a rise in the mass of food de-

Table 5. Mean delivery rates of nutrients to the nest inmates by wet weight during the incubation and nestling phases (from Table 2), adjusted for body and brood mass (BM) and nesting cycle (NC) of each hornbill species (from Table 1, see text), in Khao Yai National Park, Thailand. GH=Great Hornbill, WH=White-throated Hornbill, BH=White-throated Brown Hornbill, PH=Oriental Pied Hornbill.

Nutrient		Hornbill species, adjusted mean delivery rates (g/day, adjustment ratio from Table 1)											
		GH			WH			BH			PH		
		Before adjust	BM (2.1)	NC (1.4)	Before adjust	BM (2.5)	NC (1.4)	Before adjust	BM (1.7)	NC (1.1)	Before adjust	BM (1.0)	NC (1.0)
Protein (g/day)	Incubation	11.0	5.2	7.9	6.5	2.6	4.6	8.6	5.1	7.8	5.5	5.5	5.5
	Nestling	17.3	8.2	12.3	15.6	6.2	11.1	14.5	8.5	13.2	10.9	10.9	10.9
	Total	28.3	13.4	20.2	22.1	8.8	15.8	23.1	13.6	21.0	16.4	16.4	16.4
Fat (g/day)	Incubation	19.7	9.4	14.1	19.7	7.9	14.1	9.6	5.6	8.7	7.5	7.5	7.5
	Nestling	11.3	5.4	8.1	21.6	8.6	15.4	12.1	7.1	11.0	10.8	10.8	10.8
	Total	31.0	14.8	22.1	41.3	16.5	29.5	21.7	12.7	19.7	18.3	18.3	18.3
CHO (g/day)	Incubation	32.6	15.5	23.3	30.1	12.3	21.5	13.8	8.1	12.5	13.3	13.3	13.3
	Nestling	26.3	12.5	18.8	53.2	21.3	38.0	13.3	7.8	12.1	15.5	15.5	15.5
	Total	58.9	28.0	42.1	83.3	33.6	59.5	27.1	15.9	24.6	28.8	28.8	28.8
Ca (g/day)	Incubation	1.13	0.54	0.81	0.72	0.29	0.51	0.48	0.28	0.44	0.36	0.36	0.36
	Nestling	1.43	0.68	1.02	1.32	0.55	0.98	0.73	0.43	0.66	0.74	0.74	0.74
	Total	2.56	1.22	1.83	2.09	0.84	1.49	1.21	0.71	1.10	1.10	1.10	1.10
Energy (kJ/day)	Incubation	1,466.9	698.2	1,049.8	1,350.1	540.1	964.7	733.6	430.5	665.4	595.3	595.3	595.3
	Nestling	1,151.9	548.2	823.2	1,958.9	781.7	1,397.5	918.1	538.6	835.0	845.9	845.9	845.9
	Total	2,618.8	1,246.4	1,873.0	3,309.0	1,321.9	2,362.2	1,651.7	969.1	1,500.4	1,441.2	1,441.2	1,441.2

Table 6. Total delivery rates of nutrients to the nest inmates by wet weight (from Table 5), percentages of nutrients by body and brood mass (BM) and breeding success of each species of hornbills (from Table 1) in Khao Yai National Park, Thailand. GH=Great Hornbill, WH=Wreathed Hornbill, BH=White-throated Brown Hornbill, PH=Oriental Pied Hornbill.

Nutrient	GH (3,316 g)		WH (3,900 g)		BH (2,718 g)		PH (1,560 g)	
	Total nutrient	% by BM	Total nutrient	% by BM	Total nutrient	% by BM	Total nutrient	% by BM
Protein (g/day)	28.2	0.85	22.1	0.57	23.1	0.85	16.4	1.05
Fat (g/day)	31.0	0.93	41.3	1.06	21.7	0.80	18.3	1.17
CHO (g/day)	58.9	1.78	83.3	2.14	27.1	1.00	28.8	1.85
Ca (g/day)	2.56	0.08	2.09	0.05	1.21	0.04	1.10	0.07
Energy (kJ/day)	2,618.8	78.97	3,309.0	84.85	1,651.7	60.77	1,441.20	92.38
Breeding success (%)	93.8		66.7		92.9		95.8	

livered during the first few weeks after enclosure, a drop towards hatching time, an even higher rise until the chicks attained full size and then a drop until fledging (Fig. 1). The form of diet, whether fruits or animals, and of nutrients, whether protein, fat, carbohydrate, calcium or energy, varied between phases of the nesting cycle. Diet also varied between species and was influenced by inter-specific differences in duration of the nesting cycle and in body, clutch and brood sizes (Table 1). Due to their peculiar breeding strategy as part of which the males feed imprisoned incubating and brooding females, it is difficult to compare hornbills with other birds. However, peaks in food delivery by all four hornbill species during the early weeks of the nesting phase may be associated with the need to supply nutrients for egg production, incubation, and the commencement of molt in Week 2 for smaller species (Fig. 1c & 1d), and the restoration of any reserves used in egg production and in the regeneration of new feathers in Weeks 2–4 for larger species (Figs. 1a & 1b) (Walsberg 1983; Bryant 1997), and/or the establishment of new reserves prior to rearing chicks (Poonswad 1993).

2) Breeding cycle and nutrients

We realize that our methods for estimating nutrient delivery to nest inmates can only be applied in broad terms. We are also conscious of errors that may arise from assuming that food delivered and the nutrients analyzed match those absorbed by the female and/or chicks, especially for carbohydrates that included indigestible crude fiber (Bolton 1955) and for fruits (Levey & Matínez del Río 2001; Pryor et al. 2001).

In terms of nutrients and energy, breeding and molt are the most demanding processes within the annual cycle of any non-migratory bird species (Payne 1972;

Walsberg 1983). In hornbills, the incubation and nestling phases may be more demanding for male hornbills than for any other birds (Klaasen et al. 2003). Among the four hornbill species studied in Thailand, only the female Great Hornbill emerges midway through the nestling phase to feed herself and so reduces the workload of her mate and helps provide food for the large chick. In the White-throated Brown Hornbill, the male is assisted by non-breeding helpers, which reduced the male's workload throughout nesting by 40% (Table 1; Poonswad 1993).

We noted that delivery rates for protein by all four hornbill species rose to a peak during Weeks 2–4 of incubation (Fig. 1), as might be expected to replace resources used in egg-laying and commencement of molt. We also recorded levels for delivery of energy during incubation that were as high as during chick rearing, which may relate to the costs of female molt.

Formation of eggs requires extra quantities of protein to form albumen, fat to form yolk, protein and fat to provide energy, and calcium to form eggshells (Meijer & Drent 1999). Due to the relatively high demands of clutch production versus female maintenance in various large bird species (Meijer & Drent 1999), deposition of body reserves prior to laying would be expected in hornbills rather than an increase in food delivery.

The coincidence of nesting and complete molt of all flight feathers is uncommon in birds, but total dependence on the male hornbill for delivery suggests that food availability is high, at least for the breeding female since the breeding male only molts after nesting (Poonswad 1993). In the Great Hornbill, where the female emerges earlier in the nesting cycle than other species (Table 1), high delivery rates of protein

may also contribute to the regeneration of new feathers within a more restricted time frame. Video recordings from inside a Great Hornbill nest have shown that flight feather molt commences during Week 2 and is virtually complete by Week 10 (P. Poonswad, unpublished).

It should be noted that the most important sources of energy were fat and/or carbohydrate depending on species (Table 4). Non-significant differences in fat or carbohydrate delivery rates indicated that both were the main source of energy during the incubation and nestling phases for each species (Table 3), but from significant differences between them it seems that the amount of protein delivered was important in determining breeding success (Table 6), particularly during the seven-day pre-laying phase for production of quality eggs (Gill 1990).

Differences in nutrient delivery during the nestling phase probably reflected changes in requirements of the growing chick(s), such as for skeleton formation and feather growth (Gill 1990). In all four species there was a general increase in delivery rates during the nesting cycle, rising to a peak until chicks were expected to have completed their body growth midway through the nestling phase, followed by a drop until fledging (Fig. 1). However, this pattern did not hold for all nutrients and the exact amounts varied between species.

For example, lower fat delivery rates during the nestling phase in the Great Hornbill indicated the importance of fat for the incubating female, whereas fat was important to nestling Oriental Pied Hornbills as an energy source, possibly as a reserve to insure against poor food delivery by parents during the days just after fledging (Gill 1990).

Calcium delivery rates to incubating female Great and White-throated Brown Hornbills were as high as during the nestling phase, even though these species have different parental care strategies and brood sizes (Poonswad 1993; Table 1). Both species lay up to four eggs, thus high calcium delivery may replace that lost during egg production. Increased calcium may also help the female Great Hornbill to prepare for early emergence in Week 13, and the female White-throated Brown Hornbill to share reserves with its large brood of up to four chicks. In contrast, female Wreathed and Oriental Pied Hornbills, with similar modes of parental care but different brood sizes (Poonswad 1993, Table 1), have the whole nestling cycle to replace lost calcium, yet enjoy a significant increase in calcium delivery when the chick(s)

are growing. Calcium was derived from both fruits and animal foods, the latter were especially common in the nestling diets of White-throated Brown and Oriental Pied Hornbills with their larger broods, but some fruits, especially figs, are also known to contain calcium (Poonswad 1993; O'Brien et al. 1998), and were important in the diet of the Wreathed Hornbill throughout breeding (Poonswad et al. 1987).

3) Source of nutrients

The overall proportion of fruits and animals in the diet had been recorded for nesting hornbills (Poonswad et al. 1987), but the respective nutritional contributions of these foods were not estimated from the food types delivered.

Generally, fruit was the major source of nutrients, particularly for fat and carbohydrate. Hornbills in Khao Yai consumed as much lipid-rich fruit as those in Borneo (Leighton 1982), but whether hornbills selected lipid-rich fruits or the majority of large trees produce fruits rich in lipids remains to be studied. Differences in nutrient sources among the four Thai hornbill species were related also to feeding niche of each species. Wreathed Hornbill is a fruit specialist whereas White-throated Brown Hornbill is an animal specialist. In contrast, Great and Oriental Pied Hornbills are generalists (Poonswad 1993). Wreathed Hornbill delivers the least protein from animal sources and Oriental Pied Hornbill the most (Table 4, 5, and 6), which may affect breeding success, particularly during egg production and incubation. Wreathed and Great Hornbills feed mainly in tree canopies, but Great Hornbill was frequently observed seeking animal food. White-throated Brown Hornbill occupies the forest under-story and hunts more animal food while Oriental Pied Hornbill forages from the ground up to the canopy and consumes the greatest diversity of food among these four species (Poonswad 1993; Poonswad et al. 1998).

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ORIGINAL ARTICLE

Breeding success of the tropical Spotted Munia *Lonchura punctulata* in urbanized and forest habitats

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Abstract Information on breeding success of birds of the Indian subcontinent is almost negligible. The present study, carried out during the breeding seasons of 1997–1999 inclusive at Haridwar in northern India (29°55'N; 78°8'E), compared the breeding success of Spotted Munia *Lonchura punctulata* in urbanized and more natural forested habitats. A significant difference was found in total breeding success between the two habitats, being 48.7% in urban areas and only 31.6% in forest. Although differences in eggs hatched (70.3% vs 60.3%) and nestlings reared (57.7% vs 51.9%) were less, significantly more fledglings survived in urban areas (89.0%) than in forested habitat (70.9%). This indicates that the greater breeding success of Spotted Munia in urbanized habitats is due primarily to higher rates of post fledgling survival there. A number of factors may affect reproductive success differently between habitats. In forest, nests were built in isolated thorny trees (e.g. *Acacia nilotica*) outside of forest canopy cover. In urban areas, however, the trees or shrubs selected for nesting were mostly of introduced species (e.g. *Thuja orientalis*, *Polyanthea longifolia*), all densely foliated and rendering predation difficult. Although the typical habitat of Haridwar town is not natural, the Spotted Munia has evidently adapted quickly and successfully in its landscape. Such shifts in behaviour are not instantaneous and newly acquired behaviour takes time to spread. It would be interesting to determine whether these behavioural shifts in Spotted Munia are based on culturally transmitted learning or on genetic change.

Key words Adaptation, Breeding success, *Lonchura punctulata*

India constitutes a major part of the Oriental Realm, with wide latitudinal (08°04' to 37°60'N) and longitudinal (68°07' to 97°25'E) extents, and is situated with the tropical monsoon belt. Its varied topography, considerable insolation, and monsoon climate, impart to it enormous complexity and habitat diversity. Therefore it is possible to study the breeding biology of a wide range of birds in similar habitats and of similar/same species in diverse habitats providing an excellent opportunity for simultaneous analysis of various ecological factors. In the tropics, avian breeding seasons extend throughout the year in keeping with the extended favourable conditions; nevertheless, breeding in individual species is essentially periodic (Baker 1938; Misra 1962; Miller 1965; Thapliyal 1978; Chandola & Thapliyal 1978; Chandola et

al. 1983).

Spotted Munia (*Lonchura punctulata*) is a seasonally breeding, non-migratory waxbill (family Estrilidae) occurring throughout the Indian sub continent (Ali & Ripley 1987). It feeds mainly upon grass seeds and crop grains, which are maximally available from autumn to late spring (Ali & Ripley 1987; Bhatt 1982). The nestlings and fledglings are fed mainly with half ripe crop grains *Oriza sativa* (Sharma 2002). Prior to the onset of reproduction, food intake declines (in summer) as food becomes scarce. The food intake cycle of Spotted Munia is thus almost inversely related to its reproductive cycle (Bhatt 1982; Chandola et al. 1983). In this bird it seems that day length entrains the already existing endogenous circannual rhythm with the calendar year, thus not directly triggering the onset of breeding, as observed in many temperate birds (Bhatt 1982; Chandola et al. 1983).

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Our earlier studies indicated that in Spotted Munia the average height of the nest from the ground was 2.25 ± 0.21 meters and the shape of the nest was roughly globular or spherical with a lateral entrance hole. In this species the chicks hatch asynchronously. It has recently been observed that Spotted Munia select various introduced plants for nesting in, in urbanized habitat (Sharma 2002). With this observation in mind, we studied the breeding success in different habitats, in order to understand how successfully this species has adapted to urbanized landscapes for breeding.

STUDY AREA AND METHODS

The breeding success of the Spotted Munia *L. punctulata* was carried out from 1997 to 1999 in two different habitats (urban and forest area) in the Himalayan foothills at Hardwar ($29^{\circ}55'N$ and $78^{\circ}08'E$) India. The forest area was about 10 km away from the urban study site. The urbanized habitat is composed of residential areas, gardens, roads, ornamental trees and shrubs including *Thuja orientalis*, *Polyanthes longifolia*, *Citrus*, and *Bougainvillia* species with hedges of species such as *Pithecolobium dulce*. The forest habitat is of moist deciduous type with considerable vegetation. The main tree species in this habitat is *Sal Shorea robusta*, which comprises about 60–65% of the total vegetational cover.

During the breeding season sites were visited daily or as required. Nesting activities were observed/recorded from 6–10 m distance with the help of 7×50 binoculars, and a Sony video camera (TR590E). We recorded date of laying the first egg, date of clutch completion, clutch size, and the date of last hatching. In the urbanized area 54 eggs in 10 nests were marked with indelible Indian ink for incubational studies while 28 nests were observed for hatching success. Similarly in the forest area 60 eggs (in 10 nests) were marked and 24 nests were observed. To reduce disturbance early in the breeding cycle, incubation was recorded at fewer of the nests than the other breeding characteristics.

During the egg laying and hatching periods, nests were observed daily between 06:00 and 12:30 and from 18:00 to 20:00. The incubation period was observed using Skutch (1957) and Nice's (1954) method i.e. the period was recorded from laying of the last egg to the hatching of the same. To investigate pre- and post-fledging predation each nesting site and foraging area of the birds was inspected

twice daily and mortality/predation, if any, was recorded. In the Spotted Munia, fledglings forage along with their parents for 16–20 days and returned to their nest daily for about a week, so it was easy to watch and count the number of fledglings from each nest in this study.

In each habitat mean values of clutch size, number of hatchlings, number of nestlings that survived until fledging and number of fledglings that survived for more than one week after fledging were calculated on a per nest basis. Hatching success was calculated on the basis of the total number of eggs that were laid. Similarly, nestling fledgling and post-fledging success were calculated using the total numbers of eggs that hatched. A two way ANOVA (Baily 1995) statistical test was used to compare the data (all breeding characteristics) between forest and urban habitats and between years as well as habitat x years.

RESULTS

In the urban area a total of 54 eggs were laid in 10 nests (20 eggs in 1997, 18 in 1998, and 16 in 1999), out of which 11 eggs were destroyed by predators and 5 eggs remained unhatched due to some infection (See Table 1). The incubation period was recorded for 10 nests. The three-year average incubation period ($N=10$) was found to be 13.97 ± 0.71 (mean \pm SD) days in urban area.

Table 1. Comparison of incubation period (mean \pm SD) in Spotted Munia in urban and forest area.

Habitat	Year	No. of nests	No. of eggs	Average incubation period (days)
Urban	1997	4	20	14.66 ± 0.34
	1998	3	18	13.66 ± 0.34
	1999	3	16	13.75 ± 0.25
	3 Years	10	54	13.97 ± 0.70
Forest	1997	3	16	14.20 ± 0.70
	1998	4	22	12.50 ± 0.15
	1999	4	22	14.15 ± 0.08
	3 Years	11	60	13.30 ± 0.27
ANOVA				
Habitat	df=1	F=1.090	P>0.05	
Years	df=2	F=0.181	P>0.05	
Habitat×Years	df=2	F=3.015	P>0.05	

In the forest area a total of 60 eggs (16 in 1997, 22 in 1998, and 22 in 1999) were laid in 11 nests, out of which 6 eggs were eaten by predators and 3 eggs were found thrown out of their nests, thus 51 eggs were incubated. The three-year average incubation period (recorded from 11 nest) in the forest area was 13.30 ± 0.27 days. The two way ANOVA test indicated no variations in incubation period between habitats or years or habitat x years (Table 1).

Clutches hatched over periods of 2 to 4 days. The average hatching period in the urban area was 3.37 ± 0.85 days. Unhatched eggs were removed by parents within 2 to 3 days of the last egg hatching. In the forest area the average hatching period was 3.40 ± 0.57 days. ANOVA test indicated no variation in hatching period between habitat or years or habitat x years (Table 2).

The three-years mean clutch size was 5.66 ± 0.93 in urban habitat and 5.40 ± 0.98 in forest. There were no variations in clutch size between habitats or years or habitat x years (Table 3).

In the urban area 158 eggs were counted from 28 nests out of which 3.8% eggs were rejected by parents due to unknown factors, 22.8% were destroyed before hatching and 3.2% remained unhatched. Thus only 70.2% of all eggs hatched. In the forest area out of 131 eggs, 79 hatched. Six nests containing 34 eggs were destroyed by predators. A further 18 eggs from 9 nests remained unhatched due to infection or unknown factors. Thus the total hatching success (of 3 years) was 69.3% in the forest area. The three-years mean number of hatchlings was 3.97 ± 2.00 in the urban area and 3.26 ± 2.32 in the forest (see Table 3).

Our observations revealed 57.7% fledging success in Spotted Munia in urban habitat out of which 9.0% were eaten by predators thus survival of fledglings in urban habitat was 48.6%. In forest habitat, out of 79 eggs hatched only 41 nestlings flew indicating 51.9% nestling success, out of which 20.2% were eaten by predators. Thus only 31.6% survival of fledglings was recorded. The three-years mean of nestlings that survived until fledging was 2.28 ± 1.39 in urban habitat and 1.70 ± 1.31 in forest habitat, while the mean number of fledglings that survived for more than one week after fledging in urban areas was 1.94 ± 1.20 and in forest areas 1.03 ± 1.18 (Table 3). Two way ANOVA test indicated no significant differences in number of hatchlings between habitats or years. However, significant differences in number of fledglings and one-week surviving fledglings have been observed between habitats (Table 3).

Table 2. Comparison of hatching period (mean \pm SD) in Spotted Munia in urban and forest habitats.

Habitat	Year	No. of nests	No. of eggs	Average hatching period (days)
Urban	1997	3	13	3.25 ± 0.73
	1998	3	15	3.21 ± 0.82
	1999	2	10	3.65 ± 0.64
	3 Years	8	38	3.37 ± 0.85
Forest	1997	3	15	3.26 ± 0.68
	1998	4	21	3.10 ± 0.80
	1999	3	15	3.50 ± 0.72
	3 Years	10	51	3.40 ± 0.57

ANOVA

Habitat	df=1	F=0.016	P>0.05
Year	df=2	F=0.122	P>0.05
Habitat \times Year	df=2	F=0.544	P>0.05

DISCUSSION

It is clear from the results that the total breeding success of Spotted Munia in the urban area (48.7%) was significantly higher than in the forest area (31.6%) reflecting less predation in urban habitat than in forest. There was no difference in hatching period or clutch size between the habitats (Table 2). The maximum hatching period was 4 days. It has been suggested by some workers that the hatching of eggs over a period of several days helps in protecting the clutch and brood from the dangers of predation (Van Tyne & Berger 1959), but Lack (1947) suggested that it is an adaptation to bring brood size and available food supply into correspondence. In case of an avian species breeding success depends to a great extent on its ability to decide where and when to nest (Cody 1985; Robertson 1995). In forest habitat Spotted Munia builds nests generally on thorny plants clearly visible from the outside. Although such nests are conspicuous, nest predation by tree climbing or flying predators is largely prevented by the thorns of the trees. In the urban study area, the plants selected for nesting, such as *Ashoka pendula*, *Thuja orientalis*, *Feronia elephantum*, were dense and nests were well covered by foliage from all sides. It was therefore difficult for the predators to find the nests.

In the forest area since the predation pressure was

Table 3. Comprison of clutch size, numbers of hatchlings, fledglings and one-week surviving fledglings (mean \pm SD) in Spotted Munia in urban and forest habitat.

Habitat Year	No. of nests	Clutch size	No. of Hatchlings	No. of fledglings	No. of surviving fledglings
Urban					
1997	12	5.50 \pm 1.08	3.91 \pm 2.02	2.33 \pm 1.55	1.91 \pm 1.37
1998	7	5.70 \pm 0.75	4.00 \pm 2.00	2.42 \pm 1.27	2.14 \pm 1.06
1999	9	5.80 \pm 0.97	4.00 \pm 2.00	2.11 \pm 1.36	1.77 \pm 1.19
3 years	28	5.66 \pm 0.93	3.97 \pm 2.00	2.28 \pm 1.39	1.94 \pm 1.20
Forest					
1997	8	5.50 \pm 1.06	3.25 \pm 2.25	1.87 \pm 1.35	1.00 \pm 1.19
1998	9	5.60 \pm 1.00	3.55 \pm 2.29	1.66 \pm 1.32	1.11 \pm 1.36
1999	7	5.10 \pm 0.89	3.00 \pm 2.44	1.57 \pm 1.27	1.00 \pm 1.00
3 years	24	5.40 \pm 0.98	3.26 \pm 2.32	1.70 \pm 1.31	1.03 \pm 1.18
ANOVA—F values					
Habitat	df=1	1.104	2.629	4.549*	8.209**
Year	df=2	0.438	0.219	1.478	1.102
Habitat \times Year	df=2	0.272	0.284	0.166	0.105

*: P<0.05, **: P<0.01

high this species selected urbanized habitat for breeding purpose. It may be suggested that factors such as higher ambient temperature, greater food availability (since agricultural fields were closer to urbanized habitat) and fewer predators were contributing to enhance the breeding success of the Spotted Munia in the urban habitat. Apart from the Spotted Munia our observations on the Red-vented Bulbul *Pycnonotus cafer* also indicated that the breeding success of this species was more in urbanized habitat than forest because of low predation pressure (reduced post fledgling and adult mortality) in the urban area (Bhatt & Kumar 2003). Similarly, other avian species such as the European Woodpigeon *Columba palumbus*, Herring Gull *Larus argentatus*, Eurasian Blackbird *Turdus merula*, Mallard *Anas platyrhynchos* and Magpie *Pica pica* have been found to experience a higher breeding success in the urban environment than in wild habitat (Snow 1958; Lack 1966; Cramp 1972; Monaghan 1979; Tomialojc 1979; Bentz 1985; Kavanagh et al. 1989).

From the present study it is clear that Spotted Munia has adapted quickly and successfully to urbanized habitat, in particular in selecting introduced plants for nesting in. It may be mentioned that after breeding in urbanized habitat both parents and juveniles leave the area and spend the remainder of the year (approximately from mid November to mid

June) in agricultural and wild habitats. Which factor(s) (ultimate or proximate) stimulates the Spotted Munia to shift habitat is not currently clear but this is an interesting finding and needs further investigation.

Actually such shifts in behaviour do not occur instantly and newly acquired behaviour takes time to spread. It would be interesting to resolve whether such a shift in habitat in the Spotted Munia is based on cultural transmission, or genetic change. Here it is worth mentioning that not only the Spotted Munia but at least one other member of the same family, the White-throated Munia *L. malabarica* is also attempting to adapt to urban habitat for breeding (Sharma 2002).

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ORIGINAL ARTICLE

Notes on feeding structures of the Black-faced Spoonbill *Platalea minor*

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Abstract The bills of the spoonbills differ from the bills of most birds by being wider near the downward curved tip than in the middle, and having the mandibles dorso-ventrally extremely flattened. The mandibles have rounded lateral borders and lack cutting edges. The inward directed sides have a dense cover of thin parallel ridges on the distal parts and rows of teeth-like tubercles in the proximate parts. Their skeletons have numerous small pits in the distal parts especially along the edges and the insides. These pits are similar to the spaces for sensory corpuscles for touch in the bills of Scolopacidae (sandpipers, snipes) and are presumed to have the same function in spoonbills. The bill seems adapted for tactile feeding with lateral movements (sweeping) and for pecking, but not for probing into sediments. The wide gape with gular pouch allows the swallowing of rather large food items. The muscular layer of the gizzard is weakly developed and the gizzard is more a digestive pocket than a chewing organ such as occurs for grinding hard shells and grains in molluscivorous and granivorous birds. The long legs are laterally flattened, perhaps for minimising resistance and not-disturbing prey when walking in water during feeding; the partly webbed feet with long toes allow walking over soft mud bottoms.

Key words Bill, Black-faced Spoonbill, Digestive tract, East Asia, Leg, *Platalea minor*

Spoonbills (Ciconiiformes, Threskiornithidae) are large wading birds of 1–2 kg with long legs, necks, and bills. Their bills are remarkably widened at the tip and not pointed such as in most birds. The six spoonbill species are very similar in shape and behaviour, mainly differing in size, colour of legs, bills and other bare parts, and in distribution (del Hoyo et al. 1992). Spoonbills are considered to be tactile feeders that feed by walking in shallow water meanwhile sweeping their bills from side to side through the water (Kushlan 1978; Hancock et al. 1992). The bill is the morphological structure that is used for collecting food. In this respect, the atypical bill of a spoonbill looks clumsy compared to the bill of a chicken or egret. This has given reasons for speculations that the shape has a specific function without studying the morphology of the whole bill. That the bill can be used for sieving small prey out of sedi-

ment or water as can be done by the bills of ducks is already rejected by Allen (1942) who showed that the bill lacks the necessary rows of lamellae for sieving. Vestjens (1975) has tried to relate some relative size differences between the bills of the Royal Spoonbill *P. regia* and Yellow-billed Spoonbill *P. flavipes* and suggested that the longer bill of the latter was more suited for probing. Different speculations about the function of knobs or teeth in the mandibles were made by Allen (1942) and Vestjens (1975). That the bill can act as suction apparatus to disturb and moves benthic prey items has been suggested by Weihs and Katzir (1994) for which they specifically assumed that the upper mandible is convex in cross section. All in all, however, the mandibles have never been described in some detail, the specific feeding method of spoonbills is not well understood and there is confusion about their food. Food lists in the usual handbooks (Cramp & Simmons 1977; del Hoyo et al. 1992) give the impression that spoonbills are omnivorous, but the morphology of the alimentary tract in which the food items are processed and the legs,

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which are as well of importance for the way the food can be captured are neglected in studies about the food of spoonbills. An accurate description of the morphological structures used in collecting and processing food is an indispensable base for studying and understanding the feeding of any organism.

In this paper, we study these aspects in some detail. We focus on the Black-faced Spoonbill *Platalea minor*, which is the spoonbill species present in our study area. Its distribution is confined to East Asia where they mainly breed around the North and East Coast of the Yellow Sea and winter from South Korea to Vietnam (Kennerley 1990; del Hoyo et al. 1992; Hancock et al. 1992). We give a description of the morphology of the main feeding organs (bill, intestinal tract, and legs). The feeding method and the potential foods of the species and of spoonbills in general will be deduced from these morphological data.

MATERIALS AND METHODS

Live specimens handled were wintering Black-faced Spoonbills that had been caught in the Mai Po Marshes Nature Reserve (Hong Kong) in the winters of 1998–99 and 1999–2000, where they were marked for a migration study (Melville et al. 1999). We have discriminated first winter birds from older ones by having a pale coloured bill, totally brown iris, and the presence, distribution and size of black on the wing feathers. In adults the bill is black, the iris red, and black on the wing feathers is lacking. Intermediate specimens were considered in their second winter. Before releasing the birds, measurements were taken of morphological characteristics from adult birds of unknown sex. Length of legs were measured from the ankle (intertarsal joint) and the feathers on the belly straight to the floor in the natural stand. Bill length was measured as the shortest distance between the tip and the start of the feathering over the length axis of the upper mandible. Further details of the bill were studied from some skulls of preserved adult specimens in private collections in Hong Kong and Taiwan, and of two fledglings in a private collection in South Korea. One preserved alimentary canal was given to us in Hong Kong, it originated from a wintering specimen that was found freshly dead.

RESULTS

1) Bill

Bill length of Black-faced Spoonbills wintering in Hong Kong is 181.7 ± 13.0 mm (163–207 mm) (mean \pm SD and range; $N=22$), while the width of the spoon is 51.0 ± 2.2 mm (47–55 mm). In lateral view, the bill looks thin, is bent down near the tip and shows a 2–4 mm wide gap in the central part (Fig. 1a). In dorsal view the mandibles are wide (Fig. 1b). The upper mandible of the bill is wider than the lower in the distal part, but the lower mandible is wider than the upper in the proximal part (Fig. 1b,c). The slit-like external nostrils are close to the head in a suture that runs more or less parallel to the border of the upper mandible. The nail on the tip of the upper mandible is small and not pronounced

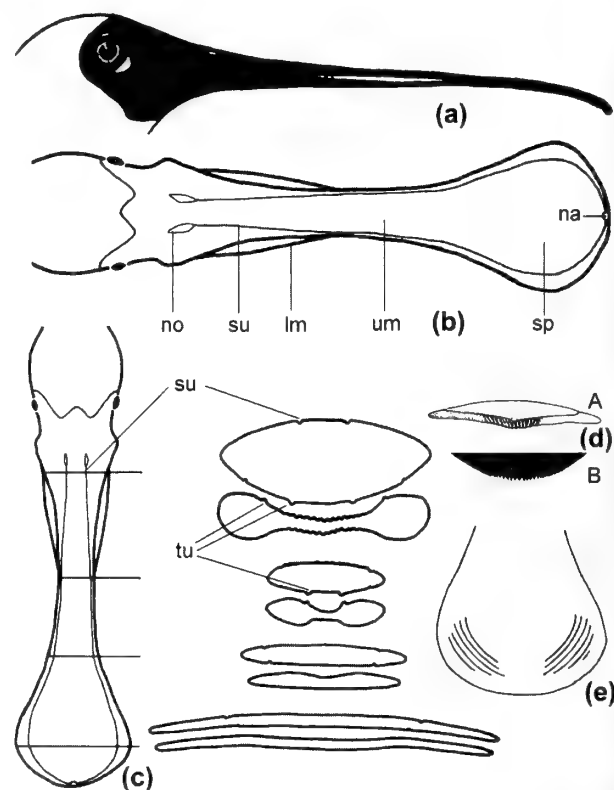


Fig. 1. (a) Lateral view of the bill showing the gap and the flatness of the mandibles. Drawn from a photograph. (b) Bill in dorsal view. (c) Cross sections of the mandibles (at the same scale). The position of the sections is indicated in the left drawing. (d) Comb-like incisions at the tip of the bill. A: Border of upper mandible in frontal view. B: Border of lower mandible dorsal view. (e) Parallel ridges on the ventral side of the lower mandible. lm: lower mandible, na: nail, no: nostril, sp: spoon, su: suture, tu: tubercles, um: upper mandible.

(Fig. 1b).

The mandibles are rigid to lateral forces, and only slightly flexible to dorso-ventral forces. Both mandibles are dorso-ventrally extremely flattened. The thickness of the spoons is 2 mm, gradually increasing proximally and reaching 7.6 ± 0.3 mm (mean \pm SD, $N=10$) in the upper mandible and 5.5 ± 0.4 mm in the lower mandible at the distal part of the nostrils (Fig. 1a, c). The epidermal layer is thin over the whole length of the mandibles, slightly thicker along the distal borders of the mandibles where both show a series of comb-like incisions on both sides of the median line (Fig. 1d A, B). A few short and inconspicuous parallel ridges are found on the outside of the lower mandible (Fig. 1e).

The insides of the mandibles are densely covered by minute (<0.5 mm high) seemingly parallel, epidermal ridges in the distal parts (Fig. 2a). The ridges split and unite during their course, and the distance between their crests varies between about 0.3 mm where they converge near the tip and 1 mm where they diverge in the widest part of the spoon. Rows of minute depressions can be seen with the help of a magnifying glass on and between the dried ridges, between the comb-like incisions, and in the smooth outer sides of the spoons of dry preserved specimens. These probably indicate sites of sensory corpuscles in the dermal layer. The central parts of the insides of the mandibles show two longitudinal rows of widely spaced, less than 1 mm high teeth-like cuticular tubercles (Fig. 2a). These tubercles are lacking in fledglings, and develop during the first winter. The lateral sides of the mandibles are rounded and lack any sign of tomia, i.e. sharp cutting edges (Fig. 1c). The two bony bars of the lower mandible are connected by soft, elastic tissue, which may expand to a gular pouch when swallowing large prey. This pouch is longitudinally folded; its colour is black in all age classes (Fig. 2a). The short tongue is triangular; the proximate side is thinly fimbriated (Fig. 2b).

The surface of the bony skeleton of the bill shows fields with small pits in the distal parts. These pits are generally wider than the holes for the blood vessels. They are most dense along the sides of the mandibles from the tip up to over half of the bill length, on the insides and the outsides of the widened distal parts (Fig. 3a A, B, C, D). Most pits have an oval aperture varying in size between 0.4×0.5 mm and 0.7×1.1 mm, and a few are round with a diameter varying between 0.3 and 0.4 mm. (Fig. 3b). Two major nerve branches run up through the bones of upper and

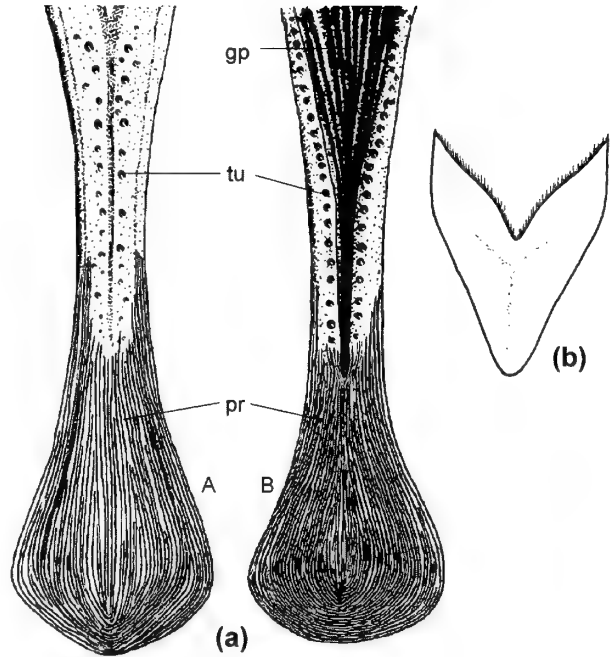


Fig. 2. (a) Inside of the bill. A: Upper mandible in ventral view. B: Lower mandible in dorsal view. (b) Tongue of Black-faced Spoonbill in dorsal view. gp: gular pouch, pr: parallel ridges, tu: tubercles.

lower mandible to the spoons and branch there.

2) Alimentary tract

The alimentary tract from a fresh carcass found in Hong Kong had deep longitudinal folds in the about 27 cm long oesophagus. The proventriculus was rather solid, about 5 cm long, 3 cm wide, and could easily be expanded. The wall mainly consisted of a layer of tubular glands (Fig. 3c D); the inside showed several (± 30 per cm^2) small openings of the glands. The ventriculus (gizzard) was about 7 cm long, 5.5 cm high and 4.5 cm wide (Fig. 3c A). The muscular layer was 9 mm thick on the dorsal side and 2 mm on the ventral and lateral sides (Fig. 3c C). Locally, it was a little thicker near the passage to the duodenum. The wrinkled touch lining of the lumen was about 5.9 mm thick along the sides and about 3 mm on the top and bottom. The intestine was 132 cm long; it had two short and narrow caeca with lumens of about 2.5 mm deep.

3) Leg

Tarsus and tibia are laterally compressed with dimensions in cross sections of 6.5 ± 0.2 mm (mean \pm SD; $N=4$) and 12.6 ± 0.1 mm, and 7.5 ± 0.2 mm and 13.5 ± 0.1 mm, respectively. The three frontal toes are

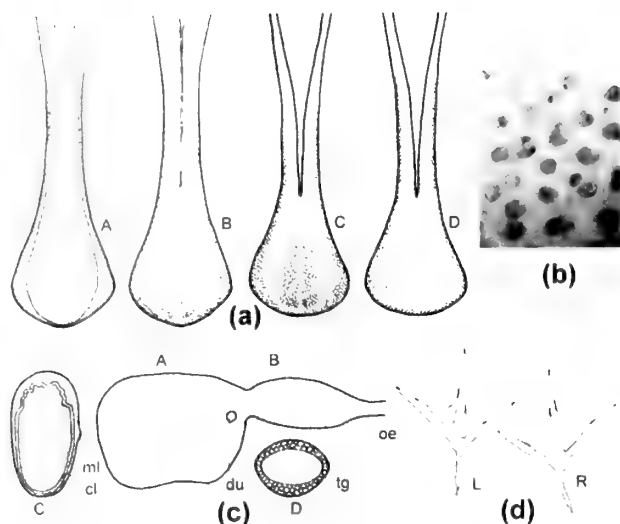


Fig. 3. (a) Distribution and relative density of pits in the bony skeleton of the mandibles of the Black-faced Spoonbill. The pits are shown as small dots. A: Upper mandible dorsal view. B: Upper mandible ventral view. C: Lower mandible dorsal view. D: Lower mandible ventral view. (b) Detail photograph of pits in the bone of the ventral side of the upper mandible. The photographed part measures 4.1×3.2 mm. (c) Stomach of a Black-faced Spoonbill. A: Ventriculus (gizzard). B: Proventriculus. C: Cross section of ventriculus. D: Cross section of proventriculus. The position of the cross sections is indicated by dotted lines. (d) Feet of Black-faced Spoonbill in ventral view. L: Left foot, R: Right foot. du: opening to duodenum, oe: oesophagus, tg: tubular glands, cl: cuticle layer, ml: muscular layer.

partially webbed (Fig. 3d); the hind toe is relatively long and has a slightly raised base, but still makes a full print in muddy sediments. The span from the tip of the nail of the middle toe to the nail of the hind toe is 141 ± 1.9 mm (mean \pm SD; $N=4$), that between the tips of the nails of left and right toes about 119 ± 1.0 mm. In the standing leg, the distance between foot sole and ankle is 130.2 ± 14.7 mm and to the belly 225 ± 22.6 mm ($N=10$).

Inspection of preserved specimens in the collection of the National Museum of Natural History, Leiden (The Netherlands) demonstrated that the bills and legs of the Eurasian, Royal, Roseate, and Yellow-billed Spoonbill show the same details as described above for the Black-faced Spoonbill. They mainly differ in length, relative width of the distal part, and colour.

DISCUSSION

The main function of a bill is collecting, tasting,

and transporting food into the oesophagus. Foods of birds differ between species and so do the bills and methods of collecting food items. The other functions such as a structure for drinking, feather preening, nest building, and defence can be conducted with all different kind of bills. Therefore we concentrate on the aspects of food collecting. The spoonbill usually feed by sweeping its bill in turbid water and preferentially at dusk and dawn (Yu & Swennen 2004a, b). We deduce that the extreme flatness of the mandibles will minimise drag and turbulence during the lateral movement while searching for prey in water. This will be mainly intended to avoid disturbing potential prey in advance because tactile feeding means that prey has to be touched by the bill and caught at once; a disturbed prey will flee from the source of disturbance and will be difficult to locate without visual clues.

The bill allows also grasping of visible food items, which is rarely noted in the Royal and Yellow-billed Spoonbill (Vestjens 1975) and Eurasian Spoonbill (Stienen & Brenninkmeijer 1993; Weihs & Katzir 1994). Feeding by probing is mentioned in the literature for the African Spoonbill (del Hoyo et al. 1992) and Yellow-billed Spoonbill (Vestjens 1975), but it is not clear what is meant. The bill shape shows that probing into sediment is not an option for any spoonbill, because the wide and curved tip would receive much resistance during penetration as well as during retraction, but when the frontal parts can be pushed into sediment the wide tip can not be opened or closed for grasping a burrowing prey, because the upper mandible has no flexible area that allows an actively upward bending of the distal part (rhynchokinesis) such as occurs in snipes (Scolopacidae) and some other bird groups.

The numerous pits in the skeleton are most likely spaces for the sensory receptors. Similar pits occur in the better-studied bills of Scolopacidae (snipes, sandpipers), but in a slightly different position (Bolze 1968; Piersma et al. 1998). Scolopacid shorebirds make sewing movements and probe into sediments for food; they have the pits for sensory corpuscles densest on the dorsal and ventral sides of the tips of the mandibles. Spoonbills make lateral feeding movements with the bill open; they have the pits relatively most dense on the lateral and insides of the bill (Fig. 3b). The most common Herbst corpuscles have a length of 0.05–0.2 mm (Schwartzkopff 1973), the pits are large enough to lodge a whole series of them similar as has been found in Red Knots (Piersma et

al. 1998). Histological evidence is still lacking, but it is supported by the presence of major nerves embedded in the skeleton. The ordering of the pits differs from the rows of supposed sensory corpuscles that are visible in the epidermis of dry preserved bills. The occurrence of such a density of supposed sensory elements agrees with the tactile way of feeding (Kushlan 1978).

The dense covering with low cuticular ridges on the insides of the distal parts of the mandibles may have a function in keeping hold of a slippery prey. All these details lead to the conclusion that the peculiar widening of the tips is necessary for improving the chance of catching moving food items that are sensed between the mandibles. This is correlated with their way of feeding in turbid water (Yu & Swennen 2004a) during twilight (Yu & Swennen 2004b) which prevent a visual detection of food items in the normal feeding situation.

The tongue is too small for a function in the upward transport of food, its role may be in covering up the glottis during swallowing and perhaps in taste. The rudimentary tongues of large fish-eaters such as occurring in the Pelicaniformes and Ciconiiformes are often considered an adaptation allowing bulky foods to be swallowed whole and quickly (McLelland 1979). The transport of food through the bill will be conducted via catch-and-throw movements. The two rows of tooth-like projections more proximal in the mandibles seem suited for holding a prey during transport to the throat, and thus replace the function of the cutting edges which give hold on a prey in other fish-eating birds. Vestjens (1975) states that these tubercles in Royal and Yellow-billed Spoonbills are also used for chewing larger food items. This is unlikely, as the projections do not have a molar-shape in any spoonbill species, and their positions in the upper and lower mandible do not match (Figs. 1c, 2a A, B). Allen (1942) suggests that these projections may contain specific sensory receptors; however, no indications of sensory elements are visible in the dried skin on and around the tubercles and there are also no sensory pits or perforations for nerves in the skeleton below the tubercles (Fig. 3a B, C).

The rudimentary tongue, gular pouch and wide, folded oesophagus indicate that rather large food items can be swallowed. The spoonbill ventriculus (Fig. 3c C) is a wide pocket for digestion suited for feeding on fish or meat. It lacks the thick muscular layer of a gizzard for grinding or cracking hard foods such as occurs in birds swallowing hard seeds or

shelled molluscs (McLelland 1979). This means that Black-faced Spoonbills can only digest meat of molluscs that have a thin shell or no shell at all. Food lists of spoonbills given in del Hoyo et al. (1992) contain in variable detail several taxa including molluscs and plants, which may largely be based on recognisable fragments in stomach contents. Shellfish is named in the second place as food of the Black-faced Spoonbill, but their anatomical structure does not support the eating of molluscs, which was also doubted for other reasons by Hsueh et al. (1993). Fragments of shells in a stomach may have been swallowed accidentally and do not represent food intake.

The length of the legs up to the belly determines the water depth in which a spoonbill can feed (Yu & Swennen 2004a). The long partly webbed toes allow walking on rather soft mud, and the lateral flattening of the legs may reduce resistance and agitation when feeding in water which may be important for not-disturbing prey.

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ORIGINAL ARTICLE

Microscopic structure and distribution of various elements in the eggshell of the Black-tailed Gull, *Larus crassirostris*, as revealed by scanning and transmission electron microscopy and X-ray compositional microanalysis

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Abstract The present paper describes the microscopic structure and distribution of various elements in the eggshell from the Black-tailed Gull *Larus crassirostris*. Scanning and transmission electron microscopy (SEM and TEM) in combination with light microscopy demonstrated four major zones in the eggshell: the shell membrane (SM), the mammillary zone (MZ), the palisade region (PR), and the cuticle layer (CL). The SM was composed of a further three layers: i.e. the limiting membrane and the inner and outer SMs consisting of thin fibers. The MZ was a layer lined with conical knobs, the mammillare, each of which had a core portion characterized by a dense matrix with a few vesicles and aggregated fine fibrils. The PR showed a spongy feature depicted as numerous vesicles embedded in a calcified matrix. The CL appeared as a simple structure different from that seen in the eggshells from other birds, such as grebes, cormorants and domestic fowl. X-ray compositional microanalysis (XCM) revealed differences in the distribution patterns of certain elements (Ca, Mg, and P) in the radial face of the eggshell. The concentration of Ca was markedly high throughout the true shell (MZ and PR), whereas that of Mg was locally high in the MZ. The concentration of P was slightly higher in the surface crystal layer of the PR than elsewhere.

Key words Black-tailed Gull *Larus crassirostris*, Distribution (Ca, Mg & P), Eggshell, Fine structure

Avian eggshells are morphologically complex structures and have long been objects of studies in poultry science, ornithology, and general biology. A considerable amount of knowledge on the morphology and physiology of eggshells has hitherto been accumulated and reviewed (Romanoff & Romanoff 1949; Gilbert 1979). The greater part of our knowledge of eggshell structure was obtained from studies on the domestic hen *Gallus gallus* (Bellairs & Boyde 1969; Fujii & Tamura 1969; Tung & Richard 1972; Tan et al. 1992; Dennis et al. 1996; Fraser et al. 1999). However, there is a growing body of data from the birds of various taxonomic groups (Tyler 1964, 1965, 1966, 1969; Becking 1975; Tullet et al. 1976; Tullet 1984; Mikhailov 1995a, b). These studies have contributed not only to comparative morphology of

the eggshells, but also to the respiratory physiology of the developing embryos (Paganelli et al. 1975; Rahn & Paganelli 1981; Tullet 1984) and consideration of avian systematics (Mikhailov 1995b). These studies have also revealed variations in the microscopic structures of eggshells and discrepancies in terminology used to describe them (Gilbert 1979; Mikhailov 1995a; Dennis et al. 1996). For a better understanding of the structural details and functional properties of avian eggshells, comprehensive studies conducted with the aid of different techniques are needed. To our knowledge, however, such studies are scanty and seem to be limited to the eggshell of domestic fowl (Tan et al. 1992; Dennis et al. 1996; Fraser et al. 1998; Richards et al. 2000).

The present study was conducted to expand our knowledge of the microscopic structure and the distribution of elements or minerals in the eggshells of wild Japanese birds by the use of modern techniques.

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For this purpose, the eggshell of the Black-tailed Gull *Larus cassirostris* was selected for sampling and investigation.

MATERIALS AND METHODS

1) Materials

Four fresh, but slightly broken, Black-tailed Gull eggs were used in this study. They were collected (by permission of the Ministry of Environment) from two abandoned nests, during a field survey of breeding colonies on the coast of the Japan Sea in the northern district of Niigata Prefecture. The nest abandonment and egg damage seemed to have been caused by mischievous intruders. The eggs were opened in the laboratory, and their contents were carefully examined and removed. The shells were then processed for microscopic observation. The eggs used were diagnosed to have been fertile and in an early stage of normal embryonic development.

2) Scanning electron microscopy

For SEM, parts of the eggshells were washed in tap water, rinsed with distilled water, cut into small pieces (about 5×5 mm), and dried for 48 hr at 38°C in an oven. Then, they were mounted on an aluminum stub, sputter-coated with platinum-palladium, and examined with a Hitachi H-800 scanning electron microscope. The rest of the eggshells were incubated overnight in a 1% solution of potassium hydroxide at 38°C to remove organic compounds from the shells, washed in tap water, rinsed with distilled water, and dried in the oven. Then, they were similarly processed and examined for comparison.

3) Light and transmission electron microscopy

For TEM, pieces of the shells were appropriately trimmed, washed briefly in tap water, rinsed with 0.1 M phosphate-buffered saline (0.01 M sodium phosphate, 0.15 M sodium chloride, pH 7.2) and fixed in a solution of 0.1 M sodium cacodylate containing 1% glutaraldehyde and 0.1 M sodium ethylenedimine-tetraacetate (EDTA), pH 7.6. For fixation and decalcification, the samples were placed in conical tubes and continuously shaken with an electric shaker. After 24 hr, the fixative was replaced with freshly prepared 0.1 M sodium cacodylate containing 0.1 M EDTA. The samples were then incubated in this medium overnight, with gentle shaking, to remove any remaining calcium. Next, they were washed three times in 0.1 M sodium cacodylate, post-

fixed for 1 hr in 0.1 M sodium cacodylate containing 1% osmium tetroxide, and washed once in 0.1 M sodium cacodylate and twice in distilled water. The samples were then dehydrated by passage through a graded ethanol series and embedded in Spurr resin. Semi-thin sections were stained with toluidine blue in borax and observed under a light microscope. Ultra-thin sections were cut with a diamond knife, stained with uranyl acetate and lead citrate, and viewed with a JEOL 1200 EX electron microscope.

4) X-ray compositional microanalysis

Pieces of the shells were embedded in epoxy resin and a radial face was polished with successively finer grades of diamond paste (final grade, 1 μ m). A final polish was given with aluminum oxide (0.3 μ m grade) as a paste in velvet supported by a plate glass. The polished surface was coated *in vacuo* with gold (ca. 30 nm) and examined with a JEOL JXA-50A electron probe microanalyzer. The electron beam (accelerating voltage, 20 kV; beam current, 0.009 μ A) was scanned along a line across the polished radial face, beginning at the shell membrane, continuing across the tip of a cone, and terminating at the plastic at the outer edge of the shell. The results on Ca, Mg, and P were recorded on a chart moving at a known speed. No examination was made of other elements, such as O or S.

RESULTS

1) Scanning electron microscopy

SEM examination of the Black-tailed Gull eggshell showed a complex architecture that differed within each of the major zones of the eggshell: the shell membrane (SM), the mammillary zone (MZ), the palisade region (PR), and the cuticle layer (CL; Fig. 1A). The SM, the innermost zone of the eggshell, was $139.7 \pm 2.4 \mu\text{m}$ (mean \pm SD, N=4) thick and consisted of three layers, i.e. the limiting membrane (LM), inner SM, and outer SM. The LM that contacts directly with the albumin of intact eggs appeared as a thin film and could be partly detached from the inner SM by utilizing a pair of forceps (Fig. 1B). The inner SM, $51.4 \pm 5.3 \mu\text{m}$ (N=4) thick, was composed of fibers that ran parallel to the eggshell surface and crossed each other at different angles. The individual fibers measured $1.2 \pm 0.2 \mu\text{m}$ (N=10) in mean diameter and had minute granular processes on its surface. The outer SM, $90.6 \pm 2.3 \mu\text{m}$ (N=10), was also composed of similar fibers, although each individual fiber

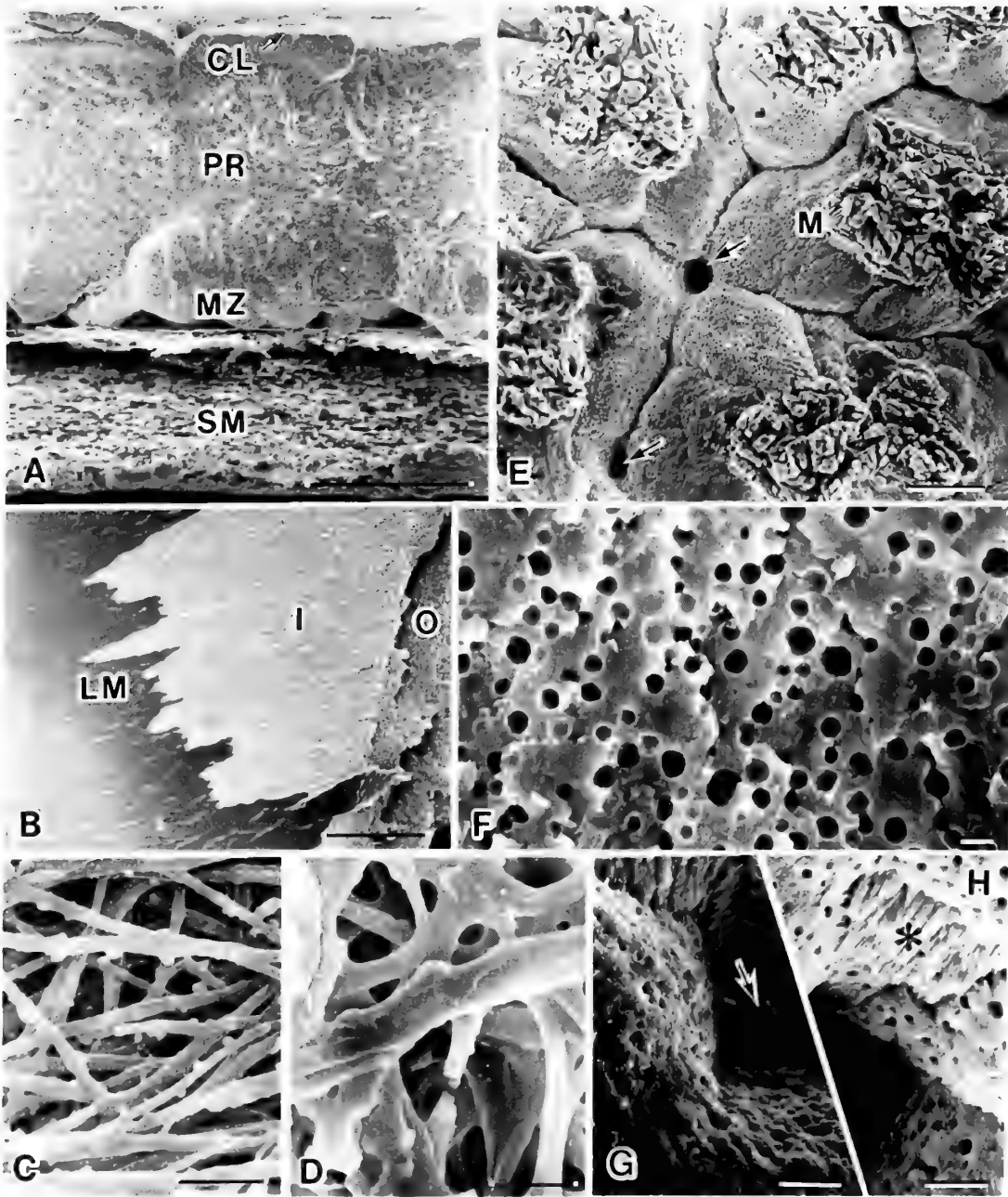


Fig. 1. SEM micrograph of an eggshell of the Black-tailed Gull *Larus crassirostris*, showing its inner and surface fine structures. (A) low-power view of radially fractured face of the eggshell, showing the cuticle layer (CL) indistinct due to low-power view, the shell membrane (SM), mammillary zone (MZ), and palisade region (PR). (B) the shell membrane consisting of the limiting membrane (LM), and inner (I) and outer (O) SMs. (C & D) details of the inner (C) and outer (D) SMs composed of thin fibers. (E) inner face of the MZ showing the mamillare (M) and internal opening (arrows) of the pore canal after maceration with potassium hydroxide. (F) closer view of the PR, showing its spongy feature owing to the numerous vesicles embedded in the calcified matrix. (G & H) closer view of the external opening of the pore canal, with (H) and without (G) maceration. In the macerated specimen (H), the densely mineralized PR with crystal structure (asterisk), is disclosed and shows a rough surface due to the removal of the CL from the shell. In contrast, the non-macerated specimen (G) shows a rather smooth surface due to the presence of the cuticle layer. Organic or cuticle substance (arrow in G) is visible in the pore canal. Scale bar = 100 μm (A & B), 50 μm (E), 5 μm (C, D, G, & H), 1 μm (F).

of the outer SM was thicker, $3.8 \pm 0.6 \mu\text{m}$ ($N=10$) in diameter, than the fibers of the inner SM and had a smooth surface (Figs. 1C, D). The border between the inner and outer SMs was usually indistinct. The MZ occupied about 25–30% of the thickness of the mineralized (calcified) portion of the eggshell, and was $79.8 \pm 2.4 \mu\text{m}$ ($N=4$) thick. It consisted of numerous conical knobs, the mammillare, the apices of which were embedded in the outer SM and, via the apices, fibers from the outer SM were connected with the mammillare (Fig. 1A). This feature of the apices was clearly shown as irregular processes and grooves in the mammillare when the shell had been macerated with potassium hydroxide solution (Fig. 1E). The PR external to the MZ had a spongy feature, being endowed with numerous vesicles ranging from 0.5 to $1.3 \mu\text{m}$ ($0.9 \pm 0.1 \mu\text{m}$; $N=4$) in diameter (Fig. 1F). Sometimes, two or more adjacent vesicles were connected to each other. Occasionally the PR showed a squamatic pattern. The external part of the PR was distinguished from the major (spongy) part of the PR; there were few vesicles, and the calcified matrix appeared to be very compact, showing an appearance of denser mineralization (Fig. 1A). This part was comparable to the external zone or surface crystal layer recognized in other species. The CL, the outermost layer of the shell, was thin ($4.1 \pm 0.4 \mu\text{m}$ thick; $N=4$) and contained occasional vesicles or minute pores. It was devoid of any microglobular structures, which were recognized within the cuticle of other avian species. The presence of the CL was confirmed by comparison of the shells with or without pre-treatment with potassium hydroxide (Figs. 1G, H).

2) Light and transmission electron microscopy

Light microscopic examination of semi-thin sections allowed characterization of the overall organic matrix architecture of the decalcified eggshells (Fig. 2A): the four major zones, SM, MZ, PR, and CL, of the eggshells were also recognized in the sections stained with toluidine blue, as already shown by SEM.

TEM examination of the SM identified the LM, about $2 \mu\text{m}$ thick, and the fibrous elements in this zone (Figs. 2B, C). The LM appeared as a heterogeneous structure consisting of electron-dense and less electron-dense materials. The LM contacted with the fibers of the inner SM without forming any special structure between them (Fig. 2B). The fibers of the inner SM showed a round or ovoid contour in cross section and had a homogeneous content of moder-

ately electron-dense material although they were associated with highly electron-dense particles (Fig. 2B). The fibers of the outer SM were thicker in diameter than those of the inner SM, but no essential difference was found in ultrastructure between them. In the apices of the mammillare, the fibers of the outer SM connected to the apices were surrounded by a mantle-like layer of less electron-dense material, from which fine fibrils projected mainly to the PR (Fig. 2C). These fibrils, 27.8 nm in mean diameter, were densely aggregated in the core portion of the mammillare, where they existed with occasional vesicles and electron-lucent flocculent material (Fig. 2D). The PR was characterized by the presence of numerous vesicles with an electron-dense fringe, $0.9 \mu\text{m}$ in mean diameter, and embedded in a matrix substance together with the flocculent material (Fig. 2E). The vesicles and the flocculent material became remarkably less dense in the external part of the PR than in the major PR zone. The CL was composed of an electron-dense amorphous material, and some parts of it were associated with a thin layer of the fibrillar elements (Fig. 2F).

3) X-ray compositional microanalysis

The distribution patterns of Ca, Mg, and P in the radial face of the eggshell were simultaneously revealed (Fig. 3). The concentration (or count) of Ca was markedly high throughout the true shell (MZ and PR), but was low or almost negligible in the SMs. In the inner zone of the shell, the concentration curve of Ca tended to be slightly reduced. On the other hand, a locally high concentration of Mg was noted immediately beneath the inner surface of the shell, approximately corresponding to the MZ. The peak Mg concentration was found in the inner part occupying about 1/6 (ca. 17%) of the total thickness of the radial face of the true shell and consisted of two indistinct peaks. In the outer part of the shell and also throughout the shell membrane, the Mg concentration was clearly low. The concentration of P was slightly higher in the surface region, corresponding to the external zone (or surface crystal layer), than in any other layers of the shell or in the SMs and tended to decline progressively toward the inner zone.

DISCUSSION

The present study on the eggshell of the Black-tailed Gull demonstrated four major zones in the radial face: the shell membranes, the mammillary zone,

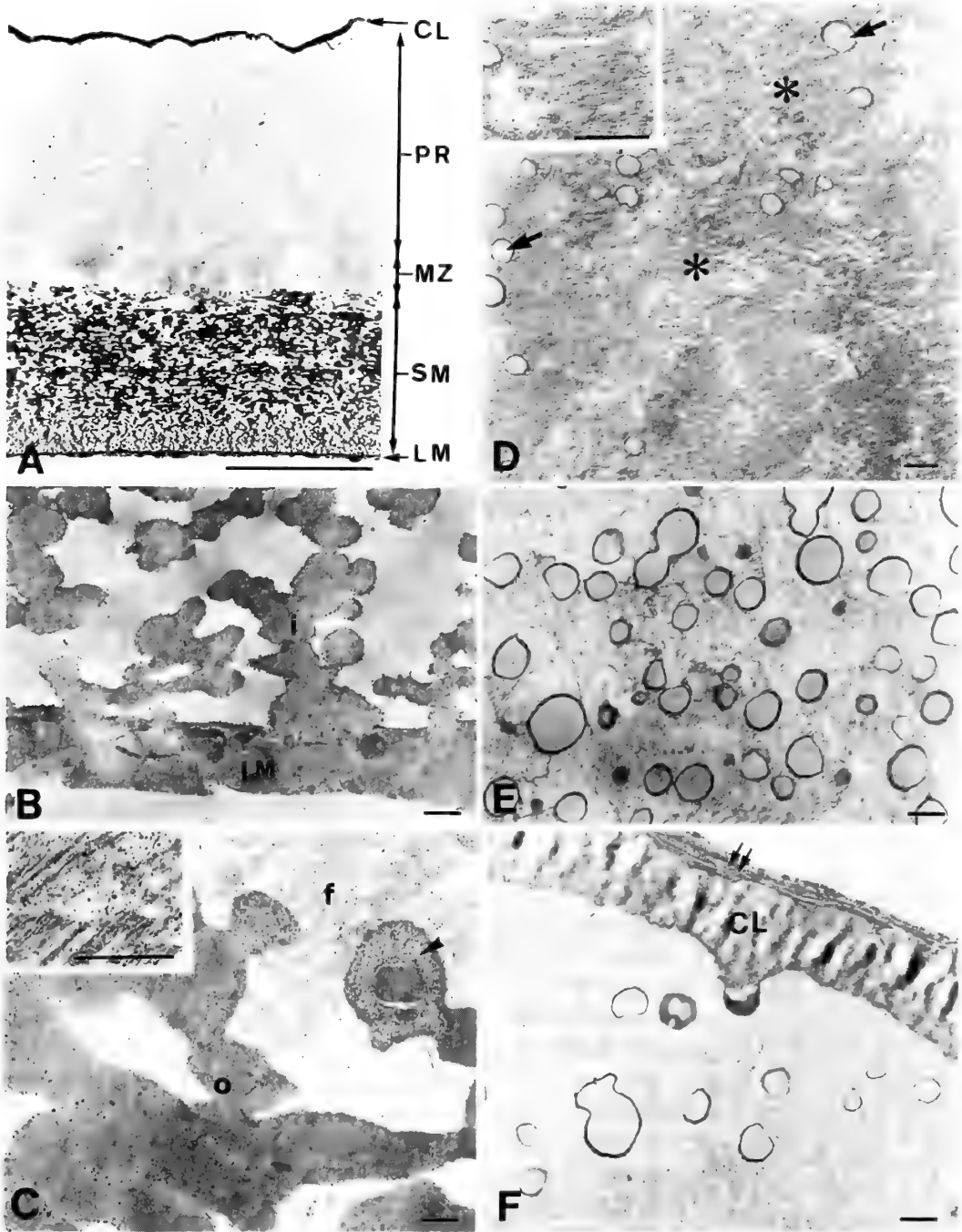


Fig. 2. Light (A) and TEM (B–F) micrographs of the decalcified eggshell. (A) cross section of full thickness of the eggshell showing the shell membrane (SM), mammillary layer (MZ), palisade region (PR), and cuticle layer (CL). (B) part of the SM showing the limiting membrane (LM) and inner SM (i). (C) part of the outer SM (o) showing fine fibrils (f) in the matrix and less electron dense mantle layer (arrowhead) of filaments. (D) core portion of the mammillare, characterized by dense aggregation of fine fibrils (asterisks) and a few vesicles (arrows). (E) part of PR of the true shell proper, showing a spongy feature depicted by numerous vesicles with an electron-dense fringe. (F) the external part of the shell, showing a few vesicles in the matrix and the cuticle layer (CL) associated with discontinuously with a thin coat consisting of fibrillar material (double arrow). Insets (C and D) show the fine fibrils. Scale bar = 100 μm (A), 1 μm (B–F).

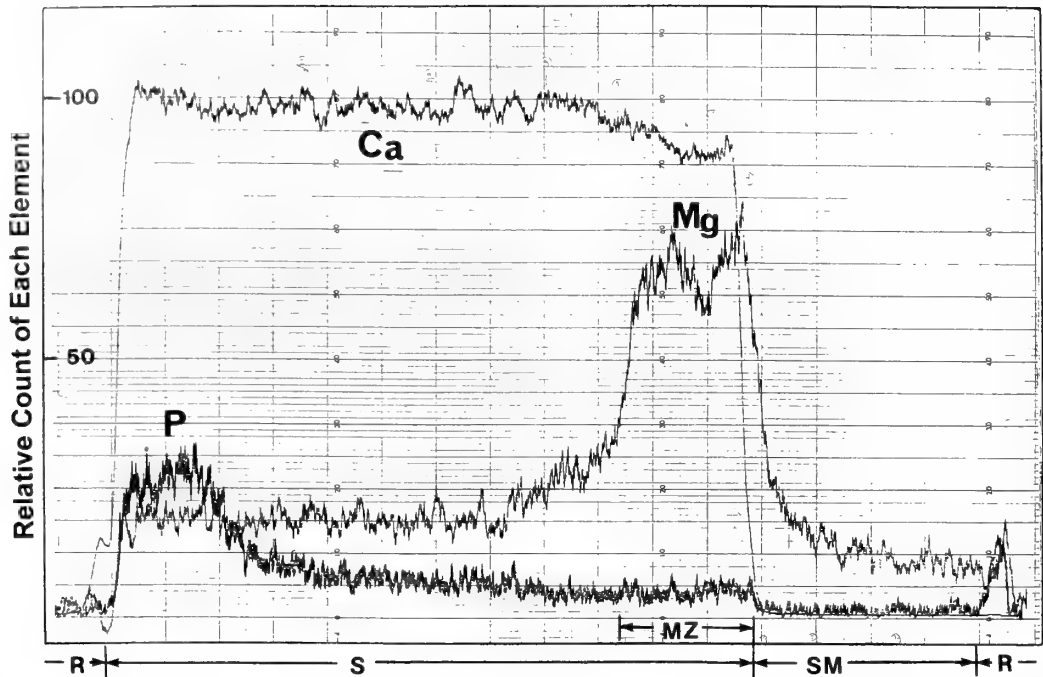


Fig. 3. Different patterns of Ca, Mg, and P concentration (counts) in the radial face of the eggshell obtained by X-ray compositional microanalysis. MZ mammillary zone; R resin as embedding material, S true shell; SM shell membrane.

the palisade region, and the cuticle layer, as recognized in the hen eggshell (Dennis et al. 1996). According to Gilbert (1979), there are generally three parts to the eggshell; the shell membranes, the testa or calcified portion, and the cuticle. The shell membranes consist of the inner membrane (*membranae testae interna*) and the more complex outer membrane (*membranae testae externa*). Similarly, Tullet (1984) recognized three layers: the shell membranes, the true shell, and the cuticle. Furthermore, the limiting membrane as the third element of the shell membranes was distinguished between the inner shell membrane and the egg albumin. According to his view, the true shell includes three parts: the cone layer, the palisade layer, and the surface crystal layer. On the other hand, Mikhailov (1995a) applied similar or even identical terms, i.e. the shell membranes, the true eggshell, and the accessory material, to the gross structure of the eggshell. At the ultrastructural level, he recognized five layers in the eggshell: the basal plate groups, the radiating elements, the squamatic zone, the external zone, and the cuticle cover. In spite of minor differences in the usage or application of the terms, the present study prefers the view of Tullet (1984), for we identified the limiting membrane and demonstrated sublayers in the true shell proper,

which correspond to the surface crystal layer and the cone layer (Tullet 1984).

TEM data on the organic parts of eggshells are few and exclusively concerned with the eggshell from the domestic fowl (Tan et al. 1992; Dennis et al. 1996; Fraser et al. 1998, 1999). The present TEM data were obtained from decalcified samples, not from intact and decalcified samples as in the domestic fowl (Dennis et al. 1996). Nevertheless, no essential difference was found in the fine structure of the shell membrane between the domestic fowl and the Black-tailed Gull. Concerning the structure and distribution of the vesicles embedded in the shell matrix, there were similarities and dissimilarities between the domestic fowl and the gull. In the gull, as in the domestic fowl, the vesicles were densely distributed in the palisade region, but scattered in the mammillary layer and the external part of the palisade region. Their size and fine structure, in particular the presence of the electron-dense fringe, were almost the same in the domestic fowl and the gull. However, the ordered stacking of co-aligned sheets of vesicles reported to exist in the domestic fowl was indistinct or almost invisible in the gull. Moreover, in the domestic fowl (Dennis et al. 1996), two types of vesicles were discerned based on their topography and internal structure, i.e.

the palisade vesicles and the crown vesicles. The vesicles in the gull, with no relation to their topography in the shell, seem to be equivalent to the palisade vesicles in the domestic fowl. The biological significance of this difference remains unknown.

The microscopic features and chemical composition of the cuticle and/or cover layers of eggshells show a considerable variation among different taxonomic groups or species. In the domestic fowl, the cuticle has a vesicular structure (Simons & Wiertz 1966) and consists of protein, fat and polysaccharides (Tyler & Simkiss 1959; Wedral et al. 1974). Such an organic cuticle was found in the eggshells of Guinea Fowl *Numida meleagris*, and the Greater Flamingo *Phoenicopterus ruber* (Tullet et al. 1976). However, among species belonging to the Gaviiformes, Pelecaniformes, and Podicipediformes, the external layer has a chalky appearance, is rich in inorganic material, and is more appropriately termed a cover rather than a cuticle (Tyler 1969; Tullet et al. 1976; Board et al. 1984). According to Tullet et al. (1976), this layer is rich in vaterite, a form of calcium carbonate. The vaterite-rich spherules in the eggshell cover of the grebes (Podicipidae) were investigated in details by X-ray compositional microanalysis and shown to contain O, Ca, P, and S (Board et al. 1984). The vaterite-containing spherules were present also in the cuticle of the hen egg (Dennis et al. 1996). Thus, the external layer of the eggshell of the Black-tailed Gull appears to be rather simple and differs considerably from that of members of the Podicipediformes, Pelecaniformes, and Galliformes. The reason for (or background causing) such a difference is obscure, but various factors may be concerned. These include, for example, the physiology of the oviduct, the life-style of the birds, and their breeding strategies in association with the microenvironment of egg-laying sites.

The markedly high concentration of Ca throughout the true shell is not surprising, because it is generally known that the avian eggshell is a biomineralized composite ceramic consisting of calcium carbonate. The higher concentration of Mg in the cone layer is, however, of particular interest. It has been generally considered that the cones or mammillares are special parts, where calcification of the eggshell initiates and ultimately the porosity and thickness of the shell are determined (Tullet & Board 1977; Tyler & Fowler 1979). Previous studies have shown two peaks in the concentration of Mg in the eggshells of galliform birds, one in the cone layer and the other at the outer edge of the shell (Itoh & Hatano 1964; Quintana &

Sandoz 1978; Board & Love 1980). In contrast, only one peak (in the cone layer) was found in the shells of many other birds (Board & Love 1980). According to Board and Love (1980), the eggshells of charadriiform birds are of the latter type, being consistent with the present results on the Black-tailed Gull. The functional significance of Mg in eggshell formation is not yet clear (Board & Love 1980), although its inhibitory role for nucleation or calcite growth during shell formation has been postulated (Bernar 1975).

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ORIGINAL ARTICLE

Amak Island Song Sparrows (*Melospiza melodia amaka*) are not evolutionarily significant

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Abstract The conservation status and evolutionary distinctiveness of the isolated, small, and endemic population of Amak Island Song Sparrows (*Melospiza melodia amaka*) have been equivocal. Coupled with a reassessment of phenotypic evidence for this taxon, we used mitochondrial cytochrome b sequences and eight microsatellite loci to evaluate the relationship of the Amak population to nearby Song Sparrow populations. Phenotypically, *M. m. amaka* is not a valid taxon, and we found that Amak Song Sparrows possess no unique haplotypes and have allele frequencies and heterozygosity values similar to those in other populations. Congruence between genetic and morphological evidence suggesting no diagnosable differences leads us to propose that this population is not an evolutionarily significant unit (ESU), not a valid subspecies, not a distinct population segment (DPS), nor a diagnosable conservation unit, but rather a sink colonized by regional source populations.

Key words Cytochrome b, Evolutionarily significant unit, *Melospiza melodia amaka*, Microsatellite, Song Sparrow

Little is known about the taxonomy, demography, or conservation status of many morphologically-based subspecies found in remote or inaccessible locations, and endemic island taxa have proven particularly susceptible to extinction in historic times (BirdLife International 2000). Song Sparrows (*Melospiza melodia*) found on tiny Amak Island (55.4°N, 163.16°W), remote and difficult to reach in the Bering Sea (Fig. 1), represent such a problematic case. The putatively nonmigratory subspecies *M. m. amaka*, known only from Amak Island, was described based on the phenotype of six specimens (Gabrielson & Lincoln 1951). After examining the few specimens existing at that time, Gibson and Kessel (1997) tentatively submerged *M. m. amaka* in subspecies *M. m. sanaka*. A single individual from Amak was included in a genetic study (mitochondrial DNA restriction fragment length polymorphisms) of Alaska's Song Sparrows (Hare & Shields 1992). These genetic data were equivocal, in that this bird possessed a haplotype found in the Aleutian Islands (Fig. 1.)

Demographic information on the Song Sparrows of Amak Island is limited. Given the size of the island (10 km²) and limited survey data, the population is small, but some evidence suggests that it fluctuates markedly in size. Although survey details such as extent of island surveyed, weather conditions, and time of day and year are insufficient to verify the conclusions, the population was considered to be extinct in 1980 (Williams & Novak 1993), and anecdotal information indicated that 25 birds were seen in 1987 and four or five in 1988 (NatureServe 2003). This suggests that Amak Song Sparrows may have experienced severe population reductions (with near-extinction events) or that the Amak population may be in effect a sink, in that it might become extinct if not for immigration from nearby populations (Hanski & Simberloff 1997). Amak Song Sparrows are not listed as threatened or endangered by the U. S. Fish and Wildlife Service, but the Nature Conservancy considers this population to be imperiled (NatureServe 2003).

Resolution of the incongruous status of this population hinges on determination of the validity of the named taxon *M. m. amaka* and its evolutionary history. Because genetic data constitute primarily neutral variation and would be unlikely to include tiny por-

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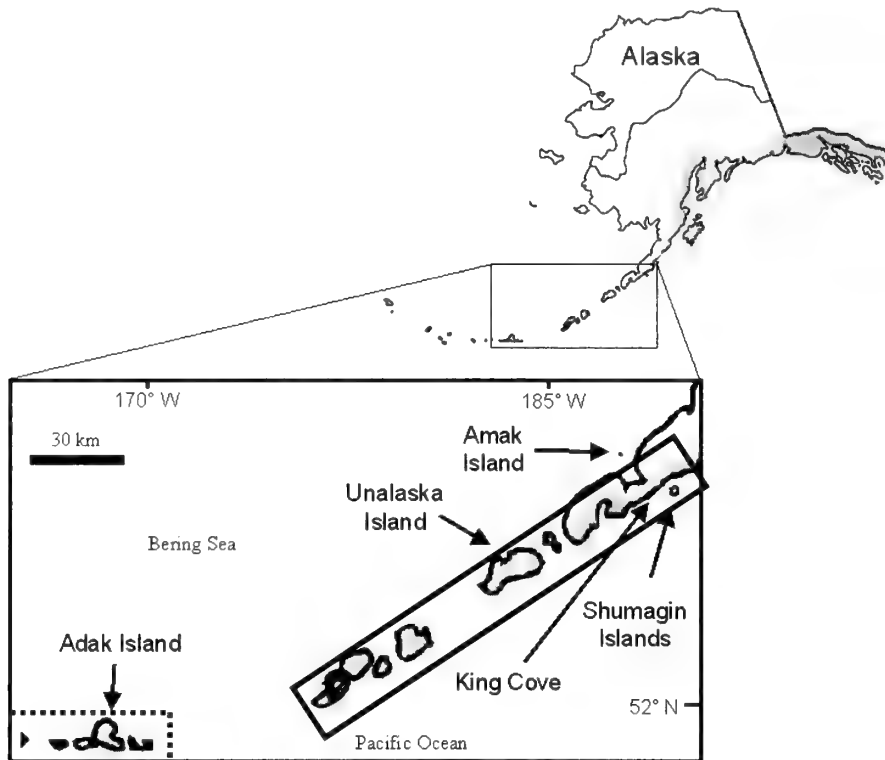


Fig. 1. Map of Alaska with Song Sparrow (*Melospiza melodia*) collection locations used in this study. Alaska distribution of Song Sparrows shaded in gray. Boxes surround subspecies ranges with *M. m. maxima* outlined with a dashed black line and *M. m. sanaka* with a solid black line.

Table 1. Location, subspecies, number of individuals sequenced, number of individuals genotyped, expected (H_e) and observed (H_o) heterozygosities and Genbank accessions for Song Sparrows (*Melospiza melodia*) used in this study. Museum voucher numbers provided in Appendix 1.

Location	Subspecies	Sequenced n	Genotyped n	H_e	H_o	GenBank accession
Amak Is., Bering Sea, Alaska	<i>amaka</i>	4	4	0.49	0.38	AY450608-611
King Cove, Alaska Peninsula, Alaska	<i>sanaka</i>	6	10	0.49	0.40	AY156406-411
Popof Is., Shumagin Is., Alaska	<i>sanaka</i>	4	9	0.56	0.49	AY156162-165
Unalaska Is., Aleutian Is., Alaska	<i>sanaka</i>	0	2	—	—	—
Adak Is., Aleutian Is., Alaska	<i>maxima</i>	10	30	0.42	0.40	AY156396-405

tions of the genome that might be under strong selection in peripheral populations, such data alone are not a reliable diagnostic tool for assessing subspecific validity (e.g., see Bulgin et al. 2003). Genetic data can provide invaluable insight into evolutionary history, however, and, when coupled with phenotypic assessments, congruent patterns between genotype and phenotype can be both insightful and diagnostic.

We reassessed phenotypic evidence and used mitochondrial (mt) DNA sequences and nuclear microsatellite loci to evaluate key questions about this little-known population: 1) Are Amak Song Sparrows

distinct from nearby populations?; and 2) Does this population show genetic evidence of severe reductions in size?

MATERIALS AND METHODS

Whole genomic DNA from 55 Song Sparrows from Amak Island and four neighboring breeding populations (Fig. 1, Table 1) were extracted following Glenn (1997). Most of the mtDNA cytochrome b gene (1,137 bp) was amplified and cycle-sequenced using four primer pairs per individual for a subset of

the extracted tissues (Table 1). Primers used included: L14851 (Kornegay et al. 1993), H16064 (Harshman 1996), L15350 (Klicka & Zink 1997), and H15424 (Hackett 1996). Amplified products were sequenced in both directions using an ABI 373A or 3100 automated sequencer (Applied Biosystems Inc., Foster City, CA). All sequences were deposited in GenBank (Table 1). All birds used in this study were sampled during the breeding season, including the four individuals from Amak. All sampled populations are considered to be non-migratory (Murie 1959). Thus, it is likely that the birds examined represented the local breeding populations at these locations.

Eight microsatellite loci were amplified for all individuals using fluorescent dye-labeled primers developed for Song Sparrows (Jeffery et al. 2001) and for two other bird species (*Escu1*, Hanotte et al. 1994; *GF5*, Petren 1998). Amplicons were screened for variation using an ABI 373A or 3100 automated sequencer. Average expected and observed heterozygosities for each population (except Unalaska) were determined using GDA (Lewis & Zaykin 2001).

Phenotypic assessment was done using new material and traditional taxonomic methods of visual comparisons of external phenotype—the same methods used in the original assessment of Amak Island Song Sparrows (Gabrielson & Lincoln 1951) and known to be effective in other drab-plumaged passerines (e.g., Winker 1997). All known existing *M. m. amaka* specimens (N=9) and several hundred each of *M. m. sanaka* and *M. m. maxima* were included in these examinations.

RESULTS

Even with new material, we did not find *M. m. amaka* phenotypically separable from *M. m. sanaka* or *M. m. maxima* using the classic “75% rule” (Amadon 1949; Patten & Unitt 2002). This is concordant with the reassessment of Gibson and Kessel (1997), in which the original material used by Gabrielson and Lincoln (1951) did not seem to support the original erection of a subspecies *amaka*. The assertion that Song Sparrows from tiny Amak Island are separable from nearby Song Sparrows at Unimak Island on the Alaska Peninsula and in the Shumagin Islands was founded on an alleged distinctness in several plumage and mensural characters in a type series of only six “adult” specimens (Gabrielson & Lincoln 1951:253). The plumage characters are equivocal: “Resembles *maxima* from the western Aleutians

in color and extensive brown markings, but somewhat more heavily marked with brown than that race both on back and breast; in most available specimens the brown markings also somewhat brighter. Closer in color to *maxima* than to the geographically closer race *sanaka*.” And neither these plumage characters nor the average culmen measurement given for the four male and two female specimens will separate with certainty even one Amak specimen from a series of adjacent *sanaka*. This equivocal situation is not at all alleviated with the new material now in the University of Alaska Museum.

Only four of Gabrielson and Lincoln’s (1951) original six specimens are present today at the U. S. National Museum, and these include the adult male holotype, a second adult male, one immature male, and one immature female (fide R. C. Banks, in litt., 2004). Thus, the original plumage description conflates both sexes and two age classes in the description of six “adults.” We think the authors should have heeded their own caveat regarding problems separating *maxima* from *sanaka* in the central-eastern Aleutians (in their description of subspecies *maxima*—published in the same article as their description of “*amaka*”): “The series of specimens in similar plumage is too limited to make a certain decision” and “The tail and wing measurements vary somewhat more than normal on account of wear and are not fully reliable” (Gabrielson & Lincoln 1951: 251–252). With such small sample sizes statistical tests are not useful where there is considerable overlap in putatively diagnostic characters. Despite the fact that plumage characters can be well assessed visually, and although we do support the subspecies concept, we find nothing phenotypically to justify continued recognition of this subspecies.

Genetically, there are no unique cytochrome b haplotypes found on Amak Island. Haplotype A is shared with Adak Island, and haplotype B is found in high frequencies at King Cove and the Shumagin Islands (Table 2; Fig. 1). There is a single unique allele (locus *Mme 12*; Fig. 2) in the Amak samples; all other alleles are found at frequencies similar to those from other sampled locations (Fig. 2). Observed and expected heterozygosities are comparable to values in other populations (Table 1).

DISCUSSION

Gibson and Kessel (1997) tentatively lumped Amak Island Song Sparrows (*M. m. amaka*) into the

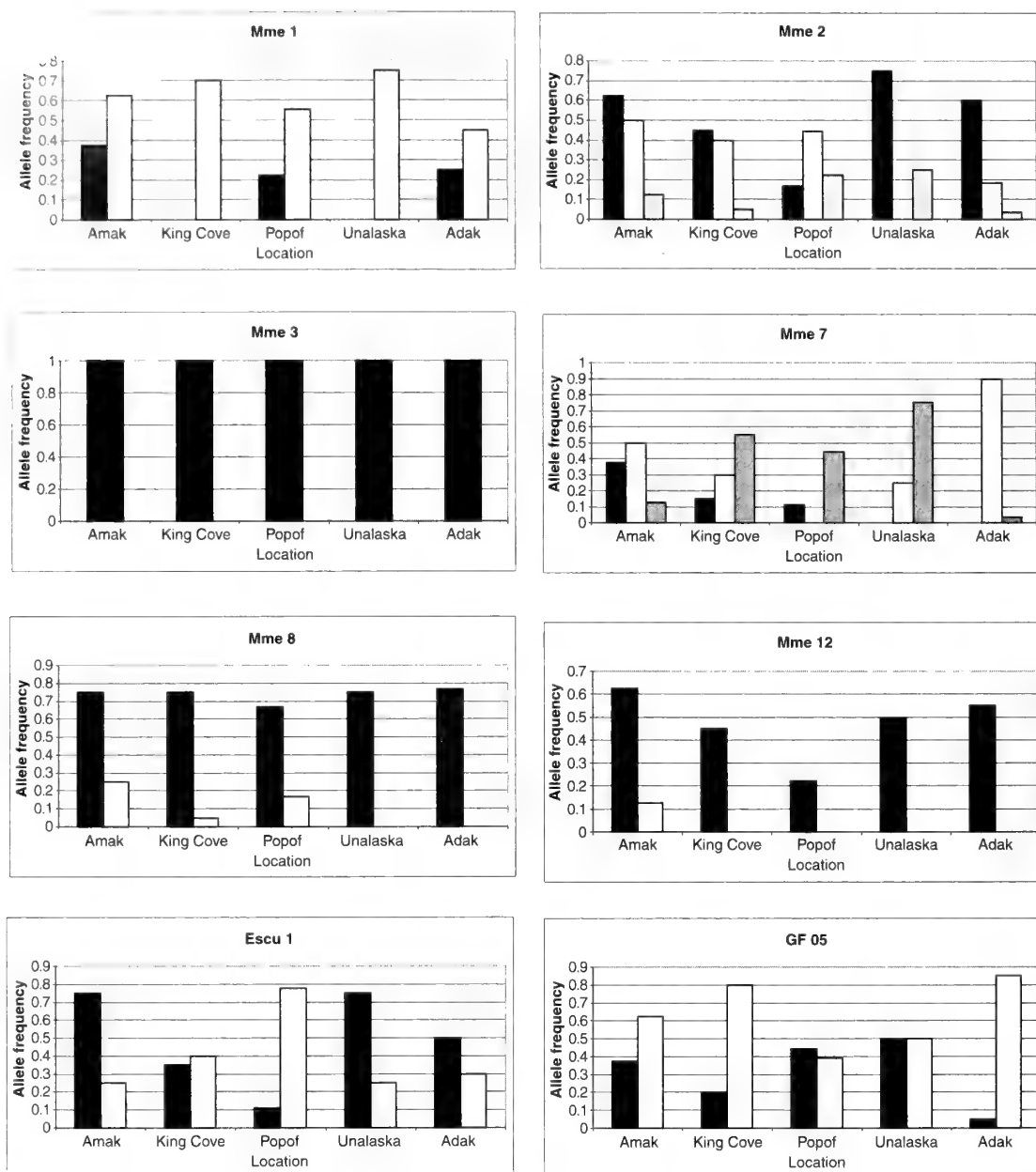


Fig. 2. Frequencies of microsatellite alleles from eight loci among Amak Island Song Sparrows and the frequencies of these alleles in other populations. Each allele is shaded differently to track its frequencies in other populations.

Table 2. Frequency of mtDNA cytochrome b haplotypes at each collection location in Alaska.

Location	Haplotype		
	A	B	C
Amak Island, Bering Sea	1	3	0
King Cove, Alaska Peninsula	0	5	1
Popof Island, Shumagin Islands	0	4	0
Adak Island, Aleutian Islands	10	0	0

neighboring subspecies, *M. m. sanaka*, which is found on the Alaska Peninsula and the eastern Aleutian Islands. Our assessment, which includes substantial new material obtained since their evaluation, supports this treatment. We recognize that sample sizes of *amaka* are small. Because this is a small population in an isolated and inaccessible location large sample sizes were not possible for this study. Given logistical and ethical constraints, these samples are not likely to be substantially increased. Only 11 spec-

imens of “*amaka*” have been collected over the last 80 years (Gabrielson & Lincoln 1951; Hare & Shields 1992; this study). We deem our evidence sufficiently conclusive to warrant reporting now for management considerations of Amak sparrows.

Genetically, Amak Song Sparrows share haplotypes with populations from two nonmigratory subspecies (*M. m. maxima* from Adak Island and *M. m. sanaka* from our other sample locations) that have no haplotypes in common. This suggests that Amak Song Sparrows might be intergrades or that this population was colonized by individuals from both subspecies. Interestingly, Gabrielson and Lincoln’s (1951) original description of *M. m. amaka* included phenotypic evidence of such intergradation.

In the Aleutian Islands and on the Pacific coast of the Alaska Peninsula, Song Sparrows are found among rocky beaches and beachside grasses (Gabrielson & Lincoln 1951, Murie 1959). Thus, Song Sparrows can only inhabit a narrow ring around Amak Island. Even if optimal conditions existed around the entire perimeter of the island (which they do not; KW pers. obs.), this population would always be small. Considering these limitations together with anecdotal suggestions of fluctuations in population size, it is likely that Amak Song Sparrows would exhibit very little genetic diversity if this population were evolutionarily isolated. Although only four individuals were sampled, heterozygosities were similar to those in other populations. This suggests that immigration to Amak from other populations is ongoing. A similar pattern was found for Song Sparrows on Mandarte Island, British Columbia (Keller et al. 2001), in which very low numbers of migrants caused a rapid recovery in a genetically bottlenecked population.

Amak Island is a small volcano that appeared above the sea about 6,700 years ago (Marsh & Leitz 1979). It is visible from the mainland coast, only 17 km away. Volcanic activity was reported in the 1700s but had ended by 1867 (Dall 1870). Thus, Amak Song Sparrows probably colonized within the last several thousand years, and subsequently they may have experienced severe ecological disturbances. Coupled with the harsh climatic conditions currently found in this region, cycles of extinction and recolonization have probably characterized this population since its founding.

The overarching question about using small sample sizes is whether larger sample sizes would alter the conclusions of the study. Phenotypically the an-

swer to this is no; new material does not bear out Gabrielson and Lincoln’s (1951) suggestion that *amaka* is a diagnosable subspecies. Nor does their original material suggest (phenotypically) that a formerly endemic population has gone extinct and been replaced by new colonists. This is in contrast to the one other subspecies that Gabrielson and Lincoln (1951) described at the same time; *maxima* is a valid subspecies (Gibson & Kessel 1997, unpubl. data).

Genetically, the four Song Sparrows from Amak shared haplotypes with adjacent populations. If more individuals were examined from Amak and were found to have other haplotypes, this would not diminish the importance of the four sparrows that possessed haplotypes found in other populations. In addition, increasing microsatellite sample sizes would likely increase the heterozygosity levels found on Amak. However, given the probable demographic shifts and the current heterozygosity values for the Amak population, it seems improbable that we would have sampled the only sparrows that were genetically diverse. Thus, gene flow would be inferred regardless of sample size.

Overall, our evidence suggests that “*amaka*” was a weak subspecies that does not hold up under scrutiny. Based on this evidence, we suggest that these birds are simply a peripheral extension of other, larger regional Song Sparrow populations. Recognition of Amak Song Sparrows as an evolutionarily significant unit (ESU), a distinct population segment (DPS), or a management unit (MU) is not warranted.

ACKNOWLEDGMENTS

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Appendix. Voucher numbers for specimens used in this study.

Subspecies	Museum ^a	Catalog numbers	Locality
<i>Melospiza melodia amaka</i>	UAM	13425–13428	Alaska: Bering Sea, Amak Island
<i>Melospiza melodia sanaka</i>	UAM	9321, 9328, 10091, 11230, 11362, 11365–66, 11381, 11389, 11823	Alaska: Alaska Peninsula, King Cove
<i>Melospiza melodia sanaka</i>	UAM	10090, 10171, 10187, 11276, 11379, 11390, 11585, 11713, 12142	Alaska: Shumagin Islands, Popof Island
<i>Melospiza melodia sanaka</i>	UAM	111238–239	Alaska: Aleutian Islands, Unalaska Island
<i>Melospiza melodia maxima</i>	UAM	8460–61, 10040–42, 10167–68, 10170, 10172, 10179, 10188, 10942, 10946–47, 11048, 11175–78, 11267–69, 11501, 11511, 11827, 11850, 12143, 13057, 13059, 13161	Alaska: Aleutian Islands, Adak Island

^a UAM = University of Alaska Museum.

ORIGINAL ARTICLE

Passerine bird pollination and fruiting behaviour in a dry season blooming tree species, *Erythrina suberosa* Roxb. (Fabaceae) in the Eastern Ghats forests, India

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ORNITHOLOGICAL SCIENCE

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Abstract *Erythrina suberosa* blooms during the dry-season. The flowers are large, papilionaceous, and partly self-compatible. The floral characteristics provide an example of ornithophilous pollination; all the flowers are pollinated exclusively by passerine birds. The fruit set rate was only 10%, but this was compensated for by a higher seed set rate. The flowers normally produce seven ovules, with those in the number two and five positions appearing to be the most preferred for seed development.

Key words Breeding system, *Erythrina suberosa*, Fruiting behaviour, Passerine birds, Pollination

Bird pollination is as important as insect pollination in the tropics and in southern temperate zones. About 100 families of flowering plants are known to have at least some members adapted for bird-pollination (Meeuse & Morris 1984). The family Fabaceae includes species pollinated by insects and others pollinated by birds; although the type of flower remains essentially similar, the bird-pollinated flowers show marked differences in structure related to this method of pollination. In insect-pollinated species, the flowers have wings and a keel forming an alighting platform for insects, which in so doing set off a remarkable trigger mechanism that delivers pollen onto the bodies of the insects. These parts of the flower are more or less suppressed when birds are the agents of pollination, and for this reason the trigger mechanism is absent in bird-pollinated species (Jaeger 1961). The genus *Erythrina* provides a typical example of bird pollination within the Fabaceae (Kumar 2000).

The genus *Erythrina* is found in the tropics and subtropics of both the New and Old Worlds (Baker & Baker 1982). Old world species are visited and pollinated by a wide range of passerine birds (Porsch 1924; Singh 1929; Ali 1932; Docters van Leeuwen 1932) whereas most New World species are probably hummingbird pollinated (Raven 1974; Toledo 1974),

however, there are also reports of various passerines visiting native species of *Erythrina* in the New World (Skutch 1954; Timkin 1970; Snow & Snow 1971; Leck 1974; Raven 1974). In India, *Erythrina* species are ornithophilous, but they are mainly visited by parrots and woodpeckers (Kumar 2000). Subramanya and Radhamani (1993) provided a list of flowering plants regularly frequented by birds based on previous works. In this list, *E. variegata* is reported to be visited by passerine and non-passerine birds whereas *E. stricta*, *E. cristagalli*, *E. suberosa* and *E. subumbrans* are visited by passerines only. However, there is no information on any *Erythrina* species regarding the floral organization, functional events of flowers in relation to the visits of birds for pollination, or fruiting behaviour. In view of this, these aspects of *E. suberosa* a common prickly tree species in the Eastern Ghats, were studied.

MATERIALS AND METHODS

Fifty-three *Erythrina suberosa* Roxb. trees were studied in the Lambasingi-Lotugedda area (17°52'N; 82°21'E), a forest stretch of about 90 km in the Eastern Ghats located at an elevation of 900 m in Visakhapatnam District, Andhra Pradesh, during February–May 2002 and 2003. Fifty flowers were sampled to record their floral morphometrics. The time of anthesis and anther dehiscence was noted by observ-

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ing marked mature buds in the field. The time and manner of anther dehiscence were noted by using a 10x hand-lens. Ten flowers were marked and bagged at the mature bud stage, opened after anthesis and nectar squeezed into a micropipette in order to measure the volume of nectar per flower; the average volume of nectar per flower was determined and expressed in μl . Pollen grain number/anther per flower was determined for 25 flowers from different individuals following the procedure in Aluri and Subba Reddi (1994). Stigma receptivity was tested with H_2O_2 according to Dafni (1992). Breeding behaviour by autogamy (bagged and hand-pollinated), geitonogamy and xenogamy, were tested through controlled pollinations following the detailed procedure in Aluri and Subba Reddi (1994). For each mode of pollination, 50 flowers (ten each) on five different trees were used. Five hundred and fifty flowers (11 each) on five different trees were tagged and followed until fruit development to observe the rate of natural fruit and seed production. A sample of 43 fruits was used to note the seed set pattern from the pedicel end to the opposite end. Flower-visitors included only birds. They were observed with binoculars and also directly when they happened to forage at close range. Their mode of approach, landing, probing behaviour, forage collected, contact with the essential organs to effect pollination, inter-tree foraging activity, damage to the flowers, if any, were all carefully observed. Furthermore, the frequency of foraging visits for each bird species was also recorded. For this, five trees with full flowering were selected and the number of times each bird species visited the tree for nectar collection from 0600 to 1800 was noted. These observations were made on the same trees on four different days in 2002 and 2003. Then, the average number of visits made by each bird species to a tree/day was calculated.

RESULTS

E. suberosa is leafless during flowering, which occurs from early March to mid-April (Fig. 1a). The flowers are produced in terminal racemes occupying only the distal half of the inflorescence axis, thus they provide suitable perches for foraging birds (Fig. 1b). The flowers mature and open acropetally. The flowers are large, 5.3 cm long, bisexual and zygomorphic (Fig. 1c). The calyx is green, campanulate and bilipped. The corolla is composed of five unequal and variously coloured petals. The corolla is characteristi-

cally papilionaceous and the petals are free. The scarlet-red standard petal is larger (4.8 cm long) and broader than the rest; it encloses the margins of the lateral pair of maroon wing petals. These are 7 mm long and overlap the margins of the greenish-maroon keel petals. The keel petals (1.1 cm long) form a carinal-like structure in which nectar is well seated. The ten stamens are diadelphous, with nine of them united into a bundle, and the tenth one free. The filaments are free towards the apex of the staminal tube and bear ditheous anthers. The stamens vary slightly in length, five are one length, four another length, and the free stamen lies below the level of the bundled stamens. The stamens are almost at the same level with respect to making contact with a bird's bill or breast as it takes nectar from a flower. The ovary is semi-inferior with one carpel having seven (rarely eight) ovules in it. The ovary is enclosed by the staminal tube, but the style protrudes through the staminal tube. The style is 11 mm long and ends in a minute stigma, and lies behind the forward level of the anthers.

The flowers open early in the morning from 0500–0600. Anthers dehisce via longitudinal slits about one hour before flowers open. Flowers produce an average of $33,870 \pm 27$ (SD) pollen grains. Nectar is secreted prior to flower opening and amounts to 140 ± 4.6 (SD) μl per flower. Nectar is well protected from direct exposure to sunlight by the keel and wing petals. The stigma is receptive to pollen from anthesis onwards and remains so until the evening of the 2nd day. The flowers remain in place for three days if not disturbed by flower visitors.

Hand-pollination tests indicated 88% pod-set occurred through xenogamy and 40% through geitonogamy, with no pod-set with autogamy (Table 1). Each fruited flower matured without abortion. Fruit development is very fast, taking only about three weeks to reach maturity. Fruit maturity and dehiscence is almost immediately followed by the initiation of leaf-flush. The natural fruit set rate was only 10% (Table 1). The fruited flowers produced 1–4 seeds with 63% produced two-seeded pods (Fig. 2). Seed set was more frequent from the ovules in numbers two and five positions in the ovary (Fig. 3). Seed set rate was 26%. Mature pods dehisce explosively (Fig. 1d) to scatter their seeds.

Twelve species of passerine birds in six families were identified as visiting flowers and taking nectar (Table 2, Fig. 1f–k). Of these, three species (Common Rosefinch *Carpodacus erythrinus*, Red-whiskered

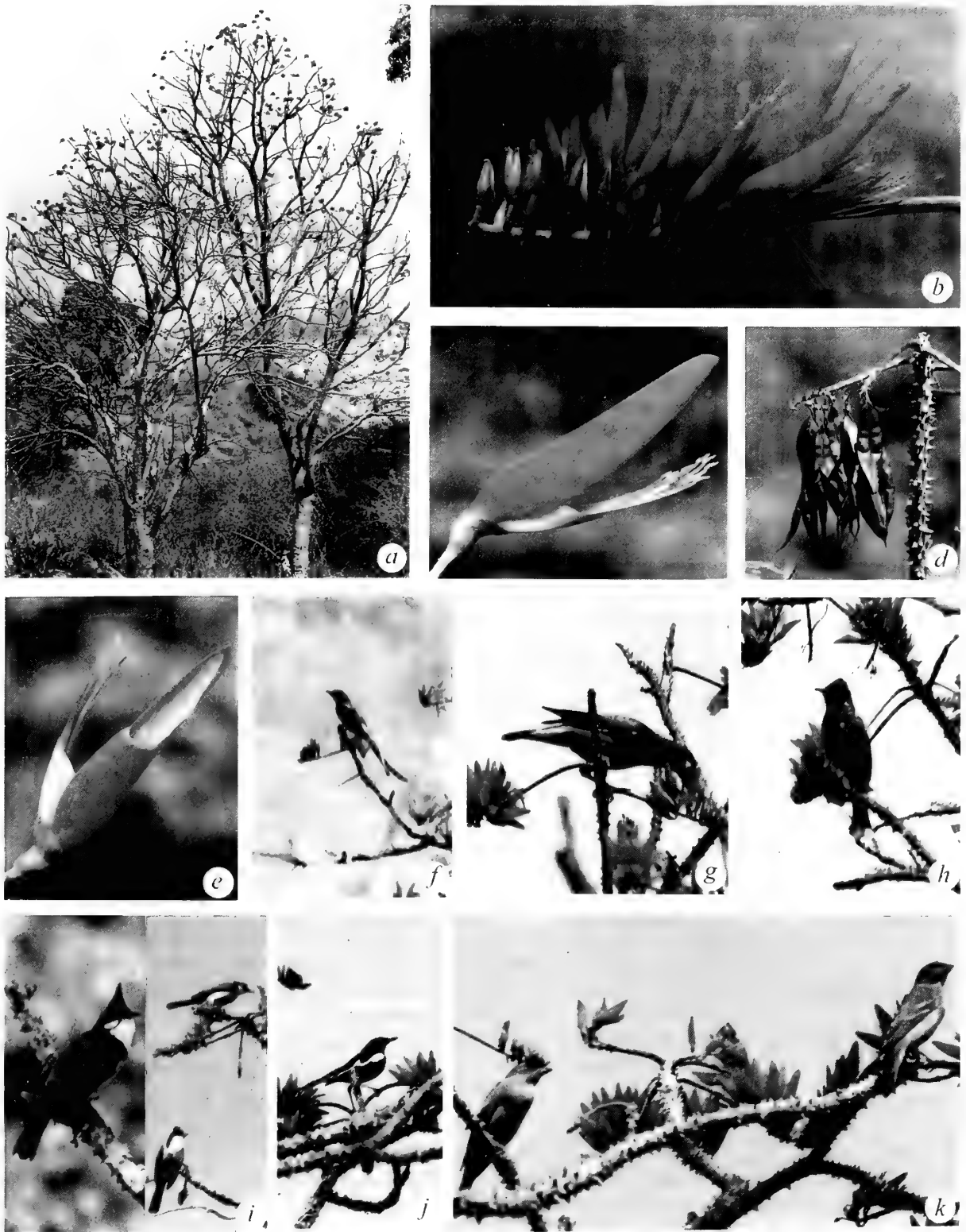
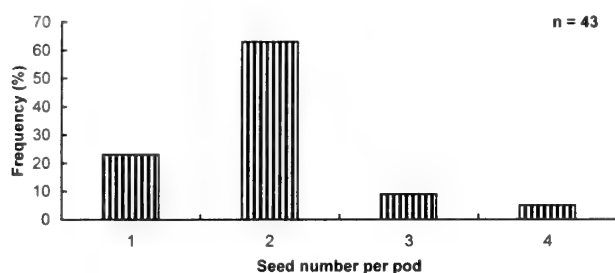
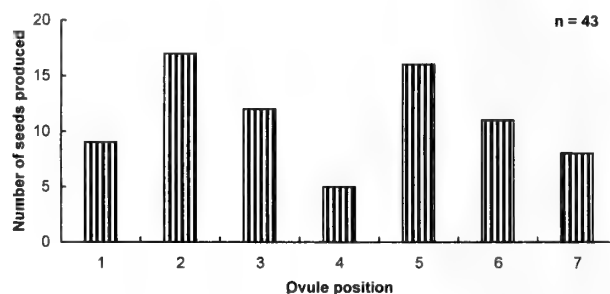


Fig. 1. *Erythrina suberosa*: a, flowering, leafless trees; b, inflorescence; c, flower; d, explosive pods; e, anterior part of standard petal cut by Black Drongo; f-k: bird visitors; f, Black Drongo; g, Indian Myna; h, Red-vented Bulbul; i, Red-whiskered Bulbul; j, Magpie-Robin; k, Common Rosefinch (left, male; right, female).

Table 1. Fruit set rate in controlled pollination treatments in *Erythrina suberosa*

Treatment	No. of flowers pollinated/tagged	No. of flowers set fruit	Percentage of fruit set
Autogamy (bagged without hand-pollination)	50	0	0
Autogamy (hand-pollinated)	50	0	0
Geitonogamy	50	20	40
Xenogamy	50	44	88
Open-pollination	550	55	10

Fig. 2. Frequency occurrence of seeds per pod in *E. suberosa*.Fig. 3. Seed production rate in relation to ovule position, from the pedicel tip in *E. suberosa*.Table 2. Passerine bird visitors to the flowers of *Erythrina suberosa*

Bird		Common name	Average no. of visits/tree/day	Percentage of visits
Family	Scientific name			
Dicruridae	<i>Dicrurus adsimilis</i>	Black Drongo	75	9
Sturnidae	<i>Sturnus pagodarum</i>	Brahminy Myna	91	10
	<i>Acridotheres ginginianus</i>	Bank Myna	16	2
	<i>A. tristis</i>	Indian Myna	69	8
	<i>A. fuscus</i>	Jungle Myna	74	8
Pycnonotidae	<i>Pycnonotus melanicterus</i>	Black-headed Yellow Bulbul	11	1
	<i>P. cafer</i>	Red-vented l Bulbu	143	16
	<i>P. jocosus</i>	Red-whiskered Bulbul	151	17
Muscicapidae	<i>Turdoides striatus</i>	Jungle Babbler	9	1
	<i>Copsychus saularis</i>	Magpie-Robin	57	7
Zosteropidae	<i>Zosterops palpebrosa</i>	White-eye	9	1
Fringillidae	<i>Carpodacus erythrinus</i>	Common Rosefinch	182	20

Bulbul *Pycnonotus jocosus* and Red-vented Bulbul *P. cafer*) made over 100 visits/tree/day; five species (Brahminy Myna *Sturnus pagodarum*, Black Drongo *Dicrurus adsimilis*, Jungle Myna *Acridotheres fuscus*, Indian Myna *A. tristis* and Magpie Robin *Copsychus saularis*) made 57–91 visits/tree/day; and the remaining four species made fewer than 20 visits/tree/day

(Table 2). All 12 species perched first on the inflorescence axis, moved toward the flower, then thrust their bill and head into the flower. While probing the flowers the birds invariably contacted the stamens and stigma with their throat or breast. After the birds took nectar, they moved backward and raised their beak to swallow nectar. The Black Drongo, however, cut the

anterior part of the standard petal to reach the nectar more easily and affected pollination (Fig. 1e). The birds visited the flowers throughout the day, but did so most often during the morning. The inflorescences were found to rock and swing when large birds such as rosefinches and mynas hopped from one inflorescence to another, and as a result withered and withering flowers fell off. Birds were found to move frequently between *E. suberosa* trees in search of more nectar, and mynas and bulbuls also visited the flowers of *Bombax ceiba* for more nectar.

DISCUSSION

Erythrina is a pantropical genus (Cruden & Toledo 1977) that shows remarkable variation in inflorescence orientation and floral organization. In paleotropical species, inflorescences are oriented horizontally and flowers are confined to the distal part of the inflorescence, providing a standing place for bird visitors. These species are described as being pollinated by passerine birds that require a standing place on the inflorescence for probing the flowers (Baker et al. 1983). In neotropical species, similar inflorescence orientation and floral organization have been reported in *Erythrina* species that have also been reported to be pollinated by passerine birds, however, there are also *Erythrina* species that are pollinated by hummingbirds. In these species, the inflorescence is almost vertical in orientation and the flowers are placed in such a way that they can be reached by hummingbirds hovering outside the flowers in order to take nectar (Baker et al. 1983). *Erythrina suberosa* is an Asian species and occurs in India. In this species, the inflorescence is oriented horizontally and the flowers occur in the distal half, providing a standing place for passerine birds for probing the flowers as reported by Baker et al. (1983) for paleotropical *Erythrina* species.

Bird-pollinated flowers open during the day, are predominantly red, odourless, and larger than insect-pollinated flowers. Their inflorescences are few in number, but they are long-lived for long-term attraction to birds. They normally have inferior ovaries, which confer protection to the ovules against the probing bills of birds. Their stamens and stigma brush against the breast or head of the visiting birds. The flowers produce copious sugary nectar, which is well protected from nectar thieves (Stiles 1978; Faegri & van der Pijl 1979; Meeuse & Morris 1984; Kumar 2000). *E. suberosa* is typically ornithophilous,

showing all of these characteristics. Furthermore, the flower of *E. suberosa* is papilionaceous with a well-developed standard petal and poorly developed wing and keel petals exposing the stamens, style and stigma to the aerial environment. The standard petal stands in an upright position and is the most conspicuous part of the flower and it is this that attracts pollinators. These characteristics have previously been reported for a range of bird-pollinated species in the Fabaceae (Jaeger 1961).

In seasonal tropical forests, many trees are pollinated by large, far-flying, systematic pollinators (Kumar 2000). *E. suberosa* trees bloom while still leafless during the dry season, when its red flowers are attractive to avian visitors. Subramanya and Radhamani (1993) reviewed information on bird and bat pollination in the Western Ghats forests of India and provided a list of birds that frequent the flowers of different plant species for nectar. They documented 15 species of passerine birds visiting the flowers of *E. suberosa* for nectar in the Western Ghats. The birds included *Dicrurus adsimilis*, *D. paradiseus*, *Acridotheres tristis*, *Corvus splendens*, *Chloropsis cochinchinensis*, *Pycnonotus jocosus*, *P. luteolus*, *Hypsipetes madagascarensis*, *Turdoides striatus*, *T. affinis*, *Orthotomus sutorius*, *Turdus merula*, *Nectarinia zeylonica*, *N. lotenia* and *N. asiatica*. All these except *H. madagascarensis* occur in the present study area (Krishna Raju 1985). Of these, birds such as *D. adsimilis*, *A. tristis*, *P. jocosus* and *T. striatus* were found to visit *E. suberosa* flowers for nectar. In addition, other passerine bird species also visited the flowers to drink nectar. All these birds perch on the proximal region of the inflorescence and move forward while probing the flowers. Acropetal anthesis of the inflorescence is an added advantage for passerine birds to probe flowers. While probing for nectar, the birds contact the stamens, style and stigma with their head or breast, which result in them being dusted with pollen and so transferring pollen between flowers. Birds have considerable energy requirements and the nectar production of one *Erythrina* tree may be insufficient for the energetic requirements of even one bird. As a result, birds are forced to make frequent visits to different trees. All of the birds we observed frequently visit different trees to quench their thirst for nectar and in so doing they effect cross-pollination.

Although hand-pollination tests indicate that *E. suberosa* is partly self-compatible, setting fruit only through geitonogamy, it is nevertheless highly cross-

compatible and shows maximum fruit set through xenogamy. This breeding system is indicative of facultative xenogamy (Cruden 1977), which essentially requires pollen vectors. Even though self-pollination can occur, most fruit set is through cross-pollination. Because, visiting birds make frequent visits to different *E. suberosa* trees and such foraging activity may result in more cross-pollen transfer. Despite the hectic foraging activity of birds, *E. suberosa* is able to produce only 10% fruit set, but this low rate is compensated for by higher seed set. Seed set pattern in the mature pods indicated that most of the pods produce only two seeds although there are seven or rarely eight ovules in the ovary. Furthermore, the positions of the developed seeds in the pods examined revealed that there is a strong positional preference for seed development; ovules in the number two and five position (from the pedicel tip to the stigmatic end) seem to produce most of the seeds. This observation does not agree with Joshi et al. (1993) who reported that positions 3, 4 and 5 may be the most preferred ones for seed development. Therefore, we suggest that further work is needed to confirm which positions of ovules are the most preferred for seed development.

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ORIGINAL ARTICLE

Offspring size as an index of habitat degradation

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Abstract Disturbances that shift a community away from its potential natural state may also degrade the quality of that community for some species. Having an index to measure changes in habitat quality resulting from such disturbances would be useful in assessing the impact of human activities on native fauna. We propose that average egg mass per clutch and offspring size for a population in a particular habitat may be a useful index of habitat quality, and perhaps degradation, for that population relative to the status of populations occupying other similar habitats in that region. We studied American Robins (*Turdus migratorius*) breeding along streams in three canyons on the western side of the Toiyabe Mountains of central Nevada, USA. The level of habitat degradation associated with cattle grazing and other human activities was determined *a priori* based on soil and understory vegetation characteristics. The density of adult birds and their body condition did not differ among canyons with differing habitat quality, nor did clutch size or brood size at day 8. However, nests containing larger eggs and chicks were associated with canyons assessed as having a higher quality, or lower level of degradation.

Key words Egg and chick size, Great Basin Desert, Habitat quality, Index, Live-stock grazing

Larger eggs typically result in heavier nestlings with greater growth rates than the young arising from smaller eggs, for at least a short period after hatching (Williams 1994). Egg size also may influence nestling survival for both precocial (e.g., Blomqvist et al. 1997) and altricial (e.g., Bolton 1991; Smith & Bruun 1998) species, although the extent of influence depends upon circumstance. Most of the variation in egg size is among rather than within clutches, and egg size can be strongly heritable (Christians 2002). Positive correlations also are seen between environmental factors and female condition and egg size (Smith et al. 1993; Potti 1999; Styrsky et al. 2002), although female size and mass alone typically explain 20% or less of the variation in the egg size within species (Christians 2002). It is not clear that there is a relationship between egg size and fitness of the re-

sulting offspring (Williams 1994). However, if larger egg size leads to larger, faster growing chicks, then these traits could result in enhanced juvenile survival and recruitment (Tinbergen & Boerlijst 1990; Cichon & Lindén 1995; Saino et al. 1997). The role of habitat quality in determining the size and number of eggs and chicks produced has been examined for a wide range of species. Whereas studies of some species indicate no link between quality of the surrounding habitat and egg size (Smith & Bruun 1998) or chick size (Hinsley et al. 1999), many have found lower habitat quality associated with decreased offspring body mass (Lens & Dhondt 1994; Verhulst et al. 1997; Turner & McCarty 1998; Hinsley et al. 1999; Huhta et al. 1999).

One of the major sources of habitat degradation in the Great Basin of the U.S.A., particularly in the riparian areas of this region, is overgrazing by livestock (Knopf et al. 1988, Fleischner 1994; Knopf & Samson 1994; Brown & McDonald 1995). The concentrated activities of domesticated animals can change vegetative structure and species composition, alter soil structure and porosity, and modifying

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stream bank morphology (Smith 1940; Ellison 1960; Brown 1978; Kauffman & Krueger 1984; Baker & Guthery 1990; Smith et al. 1994). In addition, large stretches of riparian vegetation in this region have been destroyed or degraded by water diversions, agricultural development, mining activities, and road construction (Chaney et al. 1990; Brussard et al. 1998). The effects of these activities include reduction of natural vegetation, stream channel widening, and lowered water tables (Kauffman & Krueger 1984; Platts 1991; Fleischner 1994; Belsky & Blumenthal 1997). Consequently, the structurally diverse undisturbed native riparian flora is simplified by disturbance, which in turn modifies the native bird communities typically present (Dobkin 1994; Warkentin & Reed 1999).

Although there is recognition of the links between habitat quality and size of the young produced, to our knowledge no one has proposed that features of offspring size in a particular habitat might be a useful predictor of the quality, or extent of degradation, of one habitat relative to others in the same region. We test the hypothesis that average egg mass per clutch and offspring size are potential indices of relative habitat degradation for altricial songbirds. Our work was done in riparian forests of the Great Basin, with habitat degradation determined independently *a priori* based on soil and understory vegetation characteristics.

METHODS

1) Study area

We studied American Robins (*Turdus migratorius*) breeding along three permanent streams in the relatively narrow and steeply-walled canyons on the west slope of the Toiyabe Mountains, Lander and Nye Counties, in central Nevada, USA (39°N, 117°W) in 1995 and 1996. Study areas along streams ranged in elevation from 2050–2300 m in San Juan Creek, and 2250–2600 m in Stewart and Clear Creeks. San Juan Creek lies 24 km north of Stewart and Clear Creeks and is separated from them by several ridges reaching 2800–3000 m. Stewart and Clear Creeks lie adjacent to one another, separated by a single ridge 2700 to 3000 m high. For all three creeks, the dominant riparian vegetation on the 50–200 m wide canyon floor is quaking aspen (*Populus tremuloides*) interspersed with willow (*Salix* spp.) and water birch (*Betula occidentalis*). Away from the riparian zone are steep, rocky slopes with sparse upland forests of single leaf

pinyon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and scattered patches of curl leaf mountain mahogany (*Cercocarpus ledifolius*). Primary understory shrubs include sagebrush (*Artemisia* sp.), wild rose (*Rosa woodsii*), and snowberry (*Symphoricarpos albus*). Each canyon contains grassy meadows characterized by dense cover of *Carex nebrascensis*, *C. aquatilis*, *Poa secunda*, *Juncus balticus*, or *Deschampsia cespitosa*, and extended stream banks that are used by robins for foraging and as a source of mud for nests. Length of the area sampled within each canyon was estimated using 1:50,000 topographic maps.

2) Assessing degradation

Habitat degradation was determined based on soil and understory vegetation characteristics using a ranking scheme developed by Weixelman et al. (1996). These characteristics were examined at four locations along San Juan Creek for this assessment, as well as three in both Stewart and Clear Creek canyons (D. Weixelman, D. Zamudio & K. Zamudio, U. S. Forest Service, Sparks, NV, unpubl. data). Locations were assigned an ecological status rank relative to the potential natural riparian community that would be established if successional sequences were completed without human-caused disturbances (Weixelman et al. 1996). This ecological status rank reflected high, moderate or low levels of similarity to the potential natural community. Aerial photographs were used to estimate the proportion of the study area in each canyon represented by the sample locations. To develop a quantitative value for comparing canyons, we converted these ranks for each location to a numerical score of 3, 2 or 1; a rank of 3 reflected a location with characteristics representative of the natural condition, whereas a rank of 2 indicated less similarity to the natural condition and a rank of 1 suggested limited or no similarity to natural successional patterns in the resulting community. We then calculated the average ecological status score for each canyon based on the four or three locations evaluated within each drainage.

We assessed the extent of habitat degradation in the three canyons using three additional parameters. Based on aerial photography, the percent of habitat within 100 m of each stream that contained riparian vegetation was determined, as well as the percent of riparian habitat along our study streams through which dirt roads passed or where roads defined the edge of the riparian habitat (D. Weixelman, D. Zamu-

dio & K. Zamudio, U. S. Forest Service, Sparks, NV, unpubl. data). Based on the similar topography and soil types of the three canyons, we assumed that all drainages had the same initial potential to contain riparian vegetation within the 100 m strip of land along the stream (cf. Weixelman et al. 1996). We also assumed that differences in the amount of riparian vegetation relative to other canyons were the result of different disturbance histories. Accurate grazing histories and recreational visitation rates were not available for these drainages, so dirt road cover was used as an indirect measure of road-based disturbance. Finally, we qualitatively assessed the presence or absence of severe down-cutting (streambanks with non-vegetated vertical drops ≥ 0.3 m) along significant portions of each stream.

3) Study species

The American Robin is an abundant riparian specialist in the Great Basin during the breeding season. It forages primarily on the ground, requiring a constant source of invertebrates to raise the 2–3 broods produced by each pair per year. The robin's diet and foraging ecology are relatively well studied (Sallabanks & James 1999), and nests are easily located; adults tolerate multiple nest visits (Ortega et al. 1997).

We censused adult robins and their nests in all suitable habitats along each stream. To assess relative densities of adult robins in the three canyons, from late June through early July 1996 we placed sets of 10 standard 12-m mist nets at randomly selected low, medium, and high elevation stretches in each canyon for a total of 700 mist-net hours. This timing meant that the average successful nest (based on mean clutch initiation date in each canyon) had recently fledged young. To standardize for any potential seasonal effects, all trapping events at a given elevation (i.e., low, medium, high) took place within 7 d of one another. An index of adult density was calculated as the overall capture rate per 100 net hours divided by the area of riparian vegetation in that canyon. Upon capture, adults were sexed following the criteria of Pyle et al. (1987), color banded, and their mass and tarsal length measured; age could not be reliably determined based on the criteria of Pyle et al. (1987). We tested for differences in overall body size among canyons for each sex using a Kruskal–Wallis one-way analysis of variance (ANOVA). This test was based on examining PC-1 scores from a principal components analysis (PCA) of tarsus and mass (Free-

man & Jackson 1990). The adults captured were not necessarily the birds present at nests where reproductive success variables were measured, so we could not correlate adult condition with success of a particular nesting attempt. We assumed, however, that the condition of trapped birds represented the average condition for adults, including breeding birds, in each canyon.

Nest searching was initiated on 1 June 1995 and 1 May 1996 with each canyon searched every 4–5 d through the middle of July for both years. Because we could not distinguish between first and later broods, data for all nests were pooled for these analyses. The difference between years in the start of nest searching constituted a systematic bias that would not alter comparisons between canyons across years.

Nests found before or during egg laying were revisited every 3 d until clutch completion so that clutch initiation dates, final clutch sizes, and estimated hatch dates could be determined. Nests located after clutch completion were checked every 3 d to determine hatch date. We estimated clutch initiation dates for nests found after clutch completion by subtracting the average incubation time of 13 d (Sallabanks & James 1999) from the date of hatch. When nests were discovered after hatching, we estimated clutch initiation date based on an average incubation time of 13 d in combination with chick age determined from an ageing key developed using known-age chicks (day 0 being when the first egg hatched; Warkentin et al. 2003). We compared initial clutch size and brood size at day 8 among canyons, once including all nests, and once including only those nests that had one or more chicks at day 8, using a Kruskal–Wallis ANOVA.

For all nests found during incubation with at least 3 eggs, we measured the maximum length (L) and breadth (B) of each egg to the nearest 0.1 mm using digital calipers. We converted these values to fresh egg mass (W) to assess differences in the amount of resources invested in eggs by females in different canyon types. Fresh egg mass was calculated as $W = K_w LB^2$, where K_w is a shape-specific mass coefficient reported for American Robin eggs by Hoyt (1979). Mean egg mass, as well as mass of the largest and smallest egg in each clutch were compared among canyons using Kruskal–Wallis ANOVAs.

Robin eggs hatch asynchronously with broods of three typically hatching over two days and broods of four or five hatching over three days (Slagsvold 1997). As a result, there are marked differences in

body size among individuals in a nest at a given point in the nestling phase. Therefore, we based our assessment of body size for chicks in a nest on morphological measurements from the largest chick at day 8 of the nestling phase in each nest. Interestingly, the largest individual on day 8 was not always the first to hatch because sometimes a chick's growth was retarded, apparently from extensive black fly bites. We measured mass, tarsus length, total head length, and bill length to the nearest 0.1 mm using digital calipers. These measurements were combined using PCA to develop a single measure of body size that could be used to compare chicks among canyons using a Kruskal-Wallis ANOVA. Although American Robins fledge between day 14 and 16 (Sallabanks and James 1988), we avoided handling nestlings older than 8 days to prevent premature fledging. We defined successful nests as those having at least one chick alive on day 8.

4) Statistical analyses

Clutch initiation date and fledging success data were collected and calculated for all nests encountered regardless of nestling age. Nests used in egg and chick size comparisons represent a subset of the total number of nests sampled as not all nests found were at the same stage of the breeding cycle or could necessarily be visited on day 8 to collect morphological data.

This is an exploratory assessment (*sensu* Steidl *et al.* 1997) of the predictive power of offspring size relative to habitat degradation, thus accepting $P \leq 0.10$ as statistically significant is appropriate. Where Kruskal-Wallis ANOVA indicated a significant difference among canyons for a particular variable, we conducted a post-hoc examination of the main effects. For the post-hoc test, we rank-transformed the data and then repeated the ANOVA (*cf.* Conover & Iman 1981) using Fisher's LSD to make post-hoc multiple comparisons; for these post-hoc tests we used an alpha level of 0.1. We conducted all statistical analyses using SAS version 8.12 (SAS Institute Inc. 2001).

RESULTS

San Juan Creek canyon was the most heavily degraded of the three canyons (Table 1). This canyon had the lowest area of riparian vegetation (varying from 4 to 28 m wide), in combination with the highest percentage of riparian habitat covered or bordered

by roads, the presence of severe down-cutting along significant proportions of the stream, and the lowest average ecological status score. Based on the same measures, Stewart (with a 15 to 45 m wide riparian zone) and Clear (with a 50-m wide riparian zone at all three locations examined) Creek canyons are similar in their degree of degradation, but Clear Creek may be relatively less degraded based on the higher proportion of riparian vegetation present and its higher average ecological status score (Table 1).

Data from mist-netting indicated that the density of adult robins was similar among canyons (Table 2). For adults captured, female and male size based on the PC-1 score, which explained 66.2% of the variance, did not differ among canyons when examined with a Kruskal-Wallis one-way ANOVA.

We found 90 active American Robin nests during two summers in the three canyons, of which 77 had known outcomes with eggs and/or chicks produced. There was a significant difference among canyons in clutch initiation date with nests in San Juan Creek canyon started on average 5.5 days before those in Stewart and 14.8 days before those in Clear (Table 2). Post-hoc testing suggested that nests in Clear Creek canyon were significantly later than those in the other two canyons which, in turn, did not differ from each other. The overall relationship probably reflected the significant correlation between clutch initiation date and nest elevation ($F_{1,66}=5.25$, $P=0.025$, $r^2=0.06$) across all three canyons. But since none of our parameters of interest (mean egg mass, clutch size, and

Table 1. Study site dimensions and characterization of degradation for riparian habitat in three canyons of the Toiyabe Mountain Range, Nevada. Criteria for percent habitat within 100 m of each stream that contains riparian vegetation, percent riparian area covered or bordered by roads, presence/absence of streambank down-cutting, and the ecological status score all suggest that relative degradation is least for Clear Creek and most for San Juan Creek canyons.

	Canyon		
	San Juan	Stewart	Clear
Length (m)	3505	4451	2713
Area of riparian vegetation (m ²)	84,120	137,981	135,650
Riparian area (%)	24	31	50
Riparian area bordered by road (%)	54	28	35
Severe downcutting	Present	Absent	Absent
Ecological status score	1.68	2.00	2.10

Table 2. Productivity and morphometric features of an American Robin population breeding in the riparian habitat of three canyons in the Toiyabe Mountain Range, Nevada. Values presented are mean \pm SE(n) along with statistics from Kruskal–Wallis analyses; those with different superscripted letters are significantly different from each other.

	San Juan	Stewart	Clear	χ^2	P
Adult					
Density (per 100 net-hours per km ²)	0.10	0.06	0.07		
Female PC-1	0.20 \pm 0.14 (6)	-0.26 \pm 0.36 (8)	0.16 \pm 0.42 (9)	1.26	0.53
Male PC-1	0.23 \pm 0.44 (6)	-0.36 \pm 0.32 (9)	0.09 \pm 0.28 (13)	0.67	0.71
Clutch					
Mean initiation date	May 22 \pm 2 (27) ^B	May 27 \pm 4 (26) ^B	June 5 \pm 4 (18) ^A	5.96	0.05
Initial size	3.8 \pm 0.2 (17)	3.5 \pm 0.1 (17)	3.6 \pm 0.1 (14)	1.32	0.51
Brood size at day 8	2.5 \pm 0.3 (27)	1.9 \pm 0.3 (28)	1.7 \pm 0.4 (17)	2.51	0.28
Brood size at day 8 (successful only)	3.2 \pm 0.2 (21)	3.0 \pm 0.2 (18)	3.3 \pm 0.2 (9)	0.48	0.78
Eggs					
Mean egg mass (g)	6.6 \pm 0.1 (13) ^B	6.9 \pm 0.2 (6) ^{AB}	7.2 \pm 0.1 (10) ^A	5.37	0.06
Smallest egg mass (g)	6.5 \pm 0.1 (13)	6.6 \pm 0.2 (6)	6.9 \pm 0.2 (10)	2.32	0.31
Largest egg mass (g)	6.9 \pm 0.1 (13) ^B	7.3 \pm 0.2 (6) ^{AB}	7.4 \pm 0.1 (10) ^A	5.17	0.07
Chicks					
PC-1 (largest chick)	-0.39 \pm 0.21 (12) ^B	0.23 \pm 0.39 (9) ^A	0.37 \pm 0.39 (7) ^A	4.76	0.09

chick size at day 8) were correlated with clutch initiation date ($F_{1,27}=2.68$, $P=0.11$, $r^2=0.09$; $F_{1,59}=0.41$, $P=0.52$, $r^2=0.007$; and $F_{1,24}=1.24$, $P=0.27$, $r^2=0.05$; respectively), we assumed that the effects we report on egg and chick size were not due to differences in elevation (as it affected clutch initiation date) among canyons. In addition, most research (e.g., Hochachka 1990) suggests that earlier hatching chicks are larger than those hatching later in the season. This is contrary to the trends that we report below.

Data on clutch and brood sizes suggested minimal differences among canyons in habitat quality. Initial clutch sizes, as well as brood size at day 8 for all nests and brood size at day 8 for successful nests only, did not differ significantly among canyons (Table 2). Partial-brood loss rates did not differ among canyons (Table 3; Fisher Exact Test, $P=0.66$), and likewise whole-brood loss rates did not differ among canyons (Table 3; Fisher Exact Test, $P=0.34$).

In general, eggs and chicks from nests in San Juan Creek canyon, the most degraded canyon, were smaller than those in Stewart Creek canyon, which in turn were smaller (but not significantly so) than those in Clear Creek canyon, the least degraded of the three (Table 2). Mean egg mass per clutch was 8% greater in Clear Creek canyon than those in San Juan Creek canyon and mean egg mass for Stewart Creek canyon was intermediate. Although egg mass of the smallest

Table 3. Nest outcomes for a population of American Robins breeding in the riparian habitat of three canyons in the Toiyabe Mountain Range, Nevada.

	San Juan	Stewart	Clear
Total number monitored	29	31	17
Outcome			
Failed	8	13	8
At least 1 young at day 8	21	18	9
Known partial brood loss	3	5	1
Brood size at day 8 equaled number of eggs laid	8	3	5

egg in the clutch did not differ among canyons, the largest egg in the clutch followed the same pattern as reported above for mean egg mass, with largest eggs from Clear being 7% heavier than those in San Juan (Table 2). We did not have morphometric data on specific individuals because we were not able to match eggs (i.e., egg mass) with individual nestlings, nor did we know hatching order of the young. We combined data for the four morphometric measures taken from the largest chick present in the nest at day 8 to create a PC-1 score, which explained 72% of the variance. This statistic indicated that nests in Clear Creek and Stewart canyons had the largest young and San Juan Creek canyon had significantly smaller young (Table 2).

DISCUSSION

Anthropogenic disturbances that shift a community away from its potential natural state may also degrade the quality of that community for some species. Having an index to measure changes in habitat quality resulting from such disturbances would be useful in assessing the impact of human activities on native fauna. Fluctuating asymmetry has been proposed as an index of habitat degradation based on developmental responses by individuals inhabiting a particular community (e.g., Badyaev et al. 2000; Leung et al. 2000; Lens et al. 2002; Zakharov 2003). These analyses of American Robins were complicated by limited sample size, a qualitative rather than quantitative assessment of habitat degradation, and differences amongst canyons in elevation. However, our results suggest a tendency for mean egg mass and chick size to vary with the extent of habitat degradation and thus such measures may be a useful index of habitat quality or degradation across suitable habitats within a region.

For passerines that depend on the daily accumulation of energy reserves to produce eggs (Perrins 1996), decreased availability or quality of food may cause females to allocate fewer resources to egg production. Reduced habitat quality could also be due to an increase in species that use disturbed areas, such as some competitors or predators (Paton 1994). In lower quality habitats, this could result in the production of smaller clutches and fewer young fledged (Cowie & Hinsley 1987) or lower body-mass chicks (Lens & Dhondt 1994; Verhulst et al. 1997; Hinsley et al. 1999). Our data suggest that American Robins did not alter the size of their clutch, but rather allocated less energy to each egg. In the most degraded habitat (San Juan Creek canyon) egg mass was on average 8% lower than for robin eggs from nests in the least degraded habitat (Clear Creek canyon). This difference in mean egg mass is similar to the maximum increase in egg size attributable to dietary supplements (Christians 2002).

Condition of breeding females (an index of mass relative to body size) and egg mass have been shown to be significantly correlated in a number of species (Slagsvold & Lifjeld 1989; Smith et al. 1993; Potti 1999; Styrsky et al. 2002). However, since female mass and size typically explain 20% or less of the variation in the egg size within species (Christians 2002), it appears to be the ability to translate environmental resources into egg mass that is important and

not necessarily overall body size. We trapped adults later in the season when females may have lost mass accumulated during egg laying, but we detected no difference in female size among canyons.

Some studies suggest that the effect of egg mass on chick size disappears with nestling age and is gone by the time of fledging (Magrath 1992; Smith & Bruun 1998). Smith and Bruun (1998) also found that neither egg nor nestling masses were related to the availability of high quality foraging habitat for starlings, but that this habitat variable did influence nestling survival late in the nestling period. This contrasts with our results, which indicate that there were no differences among canyons in initial clutch sizes or brood sizes at day 8. Smith and Bruun (1998) also suggested that availability of high quality habitat may only influence the translation of large egg size into large nestling size when habitat availability is limited, although egg size did not vary with availability of high quality foraging habitat in their study. Bize et al. (2002) proposed that rearing conditions, reflected by the size of eggs laid by the care-giving parent (real or foster), were more important than initial egg mass in predicting survival. The latter result contrasts with the findings of Schifferli (1973) but concurs with Reed et al. (1999) who found that survival and growth of nestlings were largely influenced by factors other than egg size.

Although measurable morphometric differences may disappear in the nestlings of some species by the time they fledge, it appears that the impact of this difference during rearing may influence the ability of an individual to obtain a high quality nesting site in the future. Verhulst et al. (1997) found that Great Tits (*Parus major*) that were relatively heavier as nestlings bred in better quality habitat as adults, and other studies suggest that these individuals will have better reproductive performance than individuals who were lighter as nestlings (Green & Cockburn 2001; Perrins & McCleery 2001; Styrsky et al. 2002).

In arid ecosystems, the presence of roads and overgrazing can adversely affect the quality of riparian habitat for some members of the biological community and lead to either population decline or loss (Fleischner 1994; Trombulak & Frissell 2000). Based on population density measures, studies of American Robins suggest that this species may actually benefit from moderate levels of habitat degradation (Page et al. 1978; Crouch 1982; Mosconi & Hutto 1982; Sedgwick & Knopf 1987; Schulz & Leininger 1991; Warkentin & Reed 1999), but examination of fitness

components in any habitat are lacking. While intensive grazing can simplify vegetation diversity and consequently cause decreased diversity of associated phytophagous insects (Lawton & Schroder 1977), moderate grazing levels may lead to enhanced foraging opportunities for robins and increased habitat quality through providing a more diverse vegetative community (Milchunas et al. 1988; Grime 1990; Collins et al. 1998) and greater diversity among those same insects groups (Eijsackers 1983; Morris 1990; Tschamntke & Greiler 1995; Oates 1995; Krueess & Tschamntke 2002). Although no canyon-level records of grazing activity are available for our study sites, we would argue that the physical features and vegetation remaining indicate that grazing pressure had been very intensive in San Juan Creek canyon. There was a low level of similarity to the potential natural community as a consequence of both cattle grazing and high levels of human use for recreational activities which together led to the lowering of habitat quality. Consequently, we propose that the invertebrate community that forms the vast majority of the diet during the breeding season for robins in this area (see Sallabanks & James 1999) would be adversely affected by grazing and human recreation resulting in a reduced invertebrate fauna and less food available to invest the resources in eggs by female robins. This degradation was reflected in decreased quality of the young robins produced in this canyon.

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SHORT COMMUNICATION

Feral cat predation on seabirds on Hahajima, the Bonin Islands, Southern Japan

ORNITHOLOGICAL
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The Bonin Islands are oceanic islands that have never been connected with the Japanese mainland, as such they remained free of terrestrial mammalian carnivores until human settlement began in 1830. Shortly thereafter, however, the domestic cat *Felis catus* was introduced to the islands by settlers and became feral (Obana 1877). The number of feral cats has increased to the point where they are now considered to have an adverse impact on the native wild birds (Kawakami 2002; Kawakami & Higuchi 2002). On Hahajima, one of the islands of the Bonin group, there are now considered to be more than 100 feral or half-feral cats ranging throughout the island (Kawakami & Higuchi 2002). Kawakami (2000) has already reported that many native birds, especially seabirds, are preyed upon by feral cats, and has speculated that seabirds are frequently targeted because they can not move quickly once they have landed.

In the Minamizaki area of Hahajima, many dead seabirds were found to show signs of being killed by feral cats. Since there is no prior information on such bird mortality from the islands, we report here on species composition, and on which parts of birds most frequently remain after predation. Since predated individuals often decompose and some parts are lost, it is not easy to assess the number of individuals involved. We propose, therefore, a convenient method for estimating the minimal number.

METHODS

The Minamizaki area (26°36'N, 142°10'E) is the southernmost cape of Hahajima (Fig. 1), and provides nesting habitat for the Brown Booby *Sula leucogaster*, which breeds there at an altitude of

10–20 m (Ministry of the Environment 1980). The area consists of open grassland with small thickets of *Pandanus boninensis* and *Scaevola frutesces*, and there are no human settlements in the area. On small islands nearby (e.g. Katsudori Island and Maru Island), Brown Boobies and Wedge-tailed Shearwaters *Puffinus pacificus* have been reported as breeding (Ministry of the Environment 1980; Chiba & Funatsu 1991).

Seabird carcasses were sought in the grassland areas of the study area once each year (Fig. 1). Surveys were conducted on 6 December 1996, 6 November 2001, 4 July 2002, 9 February 2003 and 4 February 2004, and each time carcasses were removed so as to avoid to redundant counting.

Firstly, in order to propose a convenient method for estimating the minimal number, we counted the number of main bones that were included in the dead bodies of Wedge-tailed Shearwaters, which were by far the most numerous. We selected only bones of right or left side at which more bones were found, for counting minimal number of individuals from bones of wings, legs, and shoulder girdle. This survey was conducted on the samples from 1996, 2001 and 2002.

Secondly, we counted the minimal number of dead individuals for each species for each year using the above method. Thirdly, we collected cat feces from the area and ascertained whether they included seabird feathers or not.

RESULTS

In the case of Wedge-tailed Shearwaters, wing bones, especially humeri, were found most frequently each year (Fig. 2), whereas legs were most easily lost after predation. Therefore, in order to estimate the minimal number of dead bodies, it is convenient to count the number of humerus bones.

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A total of 159 seabird remains were found: 144 Wedge-tailed Shearwaters, 9 Bulwer's Petrels *Bulweria bulwerii*, three Brown Boobies, two Tristram's Storm-petrels *Oceanodroma tristrami* and one Brown Noddy *Anous stolidus* (see Table 1). All individuals included in the samples were adults except for one immature Brown Booby found in 2001. Many bones carried tooth marks of animals, in particular almost all of the sternums examined had such marks, however, we were unable to distinguish between the marks of cats and rats, thus the identity of the predator involved was not certain. However, 45 feces of cats were found, of which 49% included seabird contour feathers identified on the basis of their morphological characters. Because of the difficulties in identifying contour feathers to species, the exact identity of the seabirds eaten by cats was not clear. Rats, insects, and crabs were also found in the feces.

DISCUSSION

A convenient method for estimating the minimum number of dead seabirds involves counting the number of wings, especially the humeri. Using this method, it was shown that many seabirds, chiefly Wedge-tailed Shearwaters, had died at Minamizaki. Furthermore, many cat feces containing seabird feathers were found in the same area. It is unreasonable to consider that so many individual seabirds had

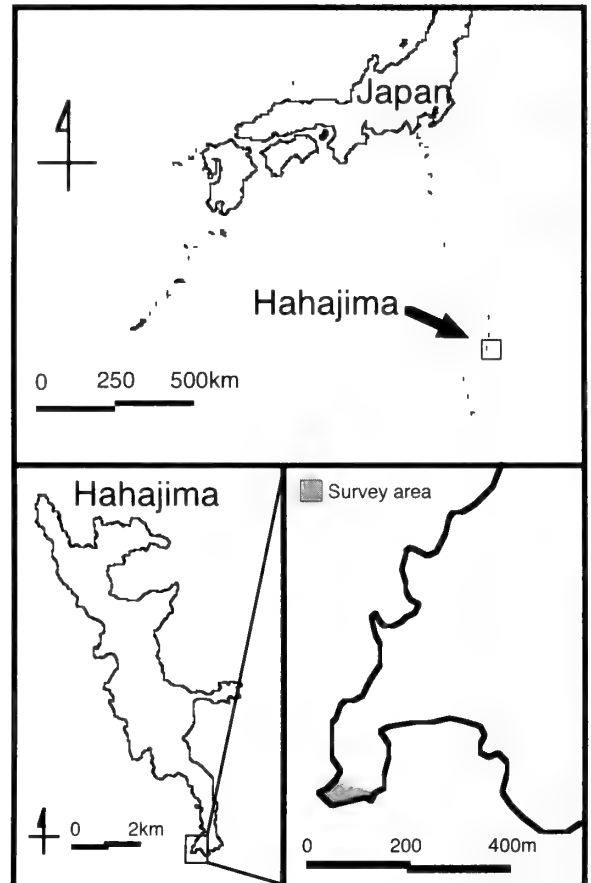


Fig. 1. The location of Minamizaki, Hahajima, the Bonin Islands, Japan. The gray area is the survey area.

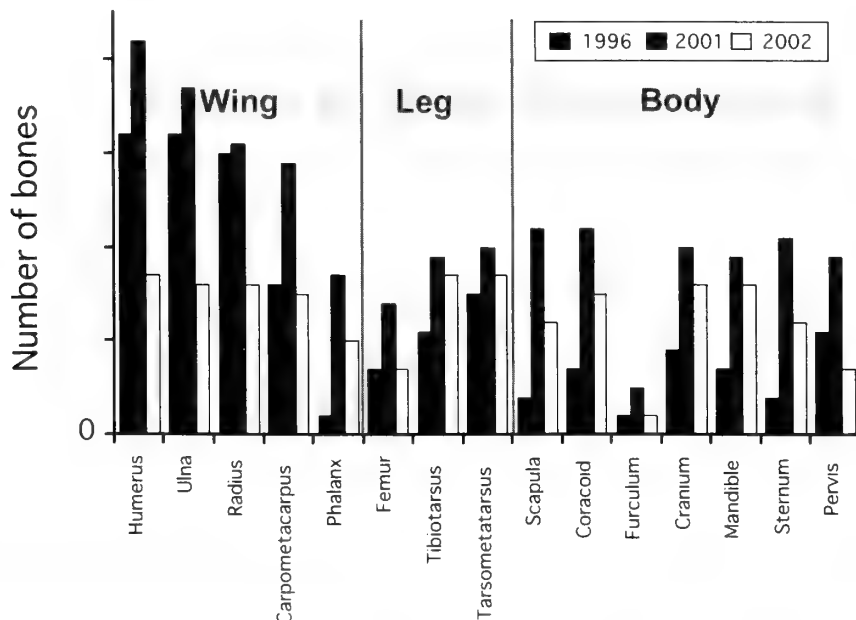


Fig. 2. The number of Wedge-tailed Shearwater bones of each type found in the Minamizaki area of Hahajima in 1996, 2001 and 2002.

Table 1. The species composition of dead birds found in the Minamizaki area of Hahajima Island.

	1996	2001	2002	2003	2004	Total
Brown Booby	0	1	1	1	0	3
Wedge-tailed Shearwater	32	42	17	28	25	144
Bulwer's Petrel	0	0	5	4	6	9
Tristram's Storm-Petrel	0	1	1	0	0	2
Brown Noddy	0	0	1	0	0	1

been eaten by cats after they had died from other causes. It seems most likely that a proportion of them at least had been killed by feral cats, after the birds had landed for some reason (such as for breeding, or to escape from bad weather). Kawakami (2000) suggested that more than half of the seabirds found dead on Hahajima had been killed by feral cats, and our results are consistent with previous data.

Hasegawa (1991) mentioned that Wedge-tailed Shearwaters, Bulwer's Petrels, Brown Boobies and Brown Noddies are observed frequently near Hahajima, with the shearwater occurring most often (about two-thirds of all seabirds observed). The species composition in our samples was roughly consistent with Hasegawa's (1991) observations. Though Brown Boobies breed in the Minamizaki area (Ministry of the Environment 1980), few remains were found in the sample. This was thought to be either because of the larger body size, or the smaller population size, of the species.

The Wedge-tailed Shearwater is the dominant seabird species in the Bonin Islands (Hasuo 1970). It was recorded to be breeding in the Minamizaki area in 1996 (H. Chiba pers. comm.), but there have been no breeding records there since, and no immature individuals were found in the samples, either. Though the relationship between the breeding failure of this species and cat predation is not proven, there is the possibility that cat predation has prevented them from breeding.

Neither Bulwer's Petrels, Tristram's Storm-petrels nor Brown Noddies have been recorded as breeding on Hahajima (Hasegawa 1991), thus the reasons for them landing in the Minamizaki area are not clear. These may have landed either because they prospected for breeding sites or because of bad weather. Seabirds sometimes land on Hahajima during bad weather (H. Chiba pers. comm.).

The feral cats in the Bonin Islands are the cause of great concern in relation to the conservation of native birds (Tokyo Regional Forest Office 1996; Kawakami

& Higuchi 2002). Among the species found dead during this study, Tristram's Storm-Petrel is listed as 'Vulnerable' in the Japanese Red Data Book, so it is especially urgent to take measures to conserve them (Ministry of the Environment 2002). Many other threatened seabirds such as Matsudaira's Storm-Petrel *O. matsudairae* and Audubon's Shearwater *P. lherminieri bannermani* also breed in the Bonin Islands and they sometimes accidentally land on the ground in bad weather making them vulnerable to cat attacks (H. Chiba pers. comm.). Thus, it is necessary to clarify the extent of feral cat predation in the islands and to control the cat population.

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SHORT COMMUNICATION

The effect of the fungus *Phellinus hartigii* on woodpecker habitat quality in Hokkaido, Japan

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Woodpeckers appear to play a keystone role in enriching tree cavity resources for forest dwellers, because cavities excavated by woodpeckers are utilized as nesting or roosting sites by many secondary cavity users, including tits, sparrows, flying squirrels, mice, and bats (e.g. Yanagawa & Muraki 2004). Woodpeckers are also considered to be indicators of forest bird diversity (Mikusiński et al. 2001). In order to develop effective management plans for woodpeckers, much information has been gathered, such as on the vegetation surrounding nest trees (e.g. Yamauchi et al. 1997; Adkins Giese & Cuthbert 2003) and the characteristics of suitable cavity trees, snags, or stubs (e.g. Runde & Capen 1987; Swallow et al. 1988; Conner et al. 1994). In addition, damage to trees caused by fungal decay has been focused on as one particular characteristic of suitable cavity trees (e.g. Runde & Capen 1987; Daily 1993). Fungi soften trunks and so reduce the energy woodpeckers require to excavate nest cavities (Conner et al. 1976).

In Hokkaido, Sakhalin Fir *Abies sachalinensis* is both a native forest species and one of the most frequently planted species in forestry plantations. One of the common tree diseases to which Sakhalin Fir is susceptible is stem sap rot caused by *Phellinus hartigii*. At first this fungus decays sapwood and then gradually invades the heartwood (Division of forest protection Hokkaido branch FFPRI 1985). Such decay occurs in up to 37% (mean=about 6%) of Sakhalin Fir trees in plantations of more than 38 years of age (Hieda 1979; S. Tsukada unpubl. data).

I hypothesized that *P. hartigii* contributes to increasing the quality of woodpecker habitat by facilitating easier excavation of nesting and feeding sites, because fungi soften Sakhalin Fir trunks and weaken their defences against wood boring insects. In this

paper, I reveal the relationship between excavations by woodpeckers and damage to Sakhalin Fir by *P. hartigii*.

MATERIALS AND METHODS

The study was conducted in a Sakhalin Fir plantation belonging to Hokkaido Forestry Research Institute, Hokkaido, Japan (43°18'N, 141°51'E; 50 m in altitude), during July 2002. The 0.8 ha plantation was 39–41 years old with a canopy height of 15 m. The environs of the study area consisted of further artificial conifer stands and farmland.

For 200 trees in the center of the study plantation, I recorded diameter at breast height (DBH), visible evidence of foraging (drilling and irregularly-shaped excavations) or that of nesting (nest or roost excavations) by woodpeckers, and visible evidence of decay damage caused by *P. hartigii*. I examined the visible evidence only on each tree trunk, and excluded the tree crown. The lower half of branches on each tree were pruned off, thus the surface of each trunk could be examined carefully, and trees utilized by woodpeckers and trees damaged by *P. hartigii* could not be missed. I included unfinished nest excavations among visible evidence of nesting because I had no reasons to explain their abandonment. Because woodpeckers excavate the entrance of the nest hole first, I defined unfinished nest excavations as finished circular entrance holes. I identified visible evidence of decay caused by *P. hartigii* based on the presence of fungal fruiting bodies or trunk groove decay. None of the trees had broken tops, nor were any dead trees included in the study.

It is not possible to identify woodpecker species based on their excavations in trees, thus this study did not discriminate among excavating woodpecker species, however, census data indicated that Great Spotted Woodpecker *Dendrocopos major* and Japan-

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ese Pygmy Woodpecker *D. kizuki* were the most common species occurring in the study area. Grey-headed Woodpecker *Picus canus* was rarely observed; White-backed Woodpecker *D. leucotos* was rarely observed during the non-breeding season and Black Woodpecker *Dryocopus martius* was a very rare and irregular winter visitor. Great Spotted and Japanese Pygmy woodpeckers were both observed in the study area during 2002.

Fisher's exact probability tests were conducted to compare the proportion of trees damaged by *P. hartigii* and excavated by woodpeckers with that of non-excavated trees. Differences in DBH between trees damaged by *P. hartigii* and those not damaged, and differences in DBH between excavated trees and non-excavated trees were identified using t-tests.

RESULTS

Trees used for nesting by woodpeckers were significantly stouter (DBH=32.0 cm \pm 4.8 SD, N=8) than non-nesting trees (DBH=28.0 cm \pm 4.6 SD, N=192, t-test: $t=2.43$, $P=0.016$), whereas trees used for foraging (DBH=30.9 cm \pm 5.9 SD, N=9) by woodpeckers did not differ significantly from those not used for foraging (DBH=28.0 cm \pm 4.6 SD, N=191, t-test: $t=1.85$, $P=0.066$), although the sample size for foraging trees was very small and the P value was nearly 0.05.

Of the 200 trees in the study area, 33 (16.5%) were damaged by *P. hartigii* and only 12 (6%) were excavated by woodpeckers. Of the 12 trees used by woodpeckers, three were nesting trees, four were feeding trees, and five were used for both nesting and feeding, and 11 of the 12 had been damaged by *P. hartigii* (the remaining 22 trees damaged by the fungus were not excavated by woodpeckers). Only one of the trees used by woodpeckers (for feeding in) had not been damaged by *P. hartigii*. On 10 of the 11 trees damaged by *P. hartigii* and also used by woodpeckers, the excavations were situated at trunk groove decay or near fungal fruiting bodies. The proportion of decay caused by *P. hartigii* in nesting trees was significantly higher than that in non-nesting trees (Fisher's exact probability test: $P<0.001$). Similarly, the proportion of decay *P. hartigii* in feeding trees was higher than that in non-feeding trees (Fisher's exact probability test: $P<0.001$).

Trees damaged by *P. hartigii* were stouter (DBH=30.1 cm \pm 4.6 SD) than non-damaged trees (DBH=27.7 cm \pm 4.6 SD, t-test: $t=2.75$, $P=0.006$). Yet there

was no significant difference in DBH between nesting and non-nesting trees damaged by *P. hartigii* (nesting=32.0 cm \pm 4.8 SD, N=8; non-nesting=29.6 cm \pm 4.4 SD, N=25, t-test: $t=1.35$, $P=0.19$). Similarly, there was no significant difference in DBH between feeding and non-feeding trees damaged by *P. hartigii* (feeding=32.4 cm \pm 4.2 SD, N=8; non-feeding=29.4 cm \pm 4.5 SD, N=25, t-test: $t=1.65$, $P=0.11$).

DISCUSSION

Woodpeckers in the Hokkaido study area were found to select Sakhalin Fir damaged by *P. hartigii* for nesting and feeding. Of the 12 trees used by woodpeckers, five (42%) were used for both nesting and foraging perhaps indicating generally overlapping preferences for activity sites. Eleven of the 12 trees utilized by woodpeckers had been damaged by the fungus and most of the excavations were situated at sites of trunk groove decay or near fungal fruiting bodies. The fungus *P. hartigii* appears to contribute to increasing woodpecker habitat quality, both for nesting and feeding sites in Hokkaido. In terms of nest site selection, similar relationships have also been found between fungi and avian excavators in North America, where, for example, Daily (1993) found a relationship between Red-naped Sapsucker *Sphyrapicus nuchalis* and *Formes ignarius* var. *populinus* and where Steeger and Hitchcock (1998) found a relationship between Red-breasted Nuthatch *Sitta canadensis* and *Armillaria ostoyae* root disease.

I did not examine the possibility that fungal decay may follow woodpecker damage. Damaged trees are generally infected from dead branches or during injuries caused during thinning operations (Matsumoto 1965; Hieda 1979). Thus fungal decay is generally considered to precede woodpecker damage.

Hieda (1979) reported that among same age trees, Sakhalin Fir trees damaged by *P. hartigii* were larger than non-damaged trees; a finding confirmed during this study. Trees used by woodpeckers as nesting trees or as feeding trees tended to have greater DBHs than trees not used by woodpeckers. It seems that these preferences do not result from woodpeckers simply selecting larger trees, because almost all of the trees used by woodpeckers were infected with *P. hartigii*. Furthermore, trees used by woodpeckers and also infected with *P. hartigii* were not larger than infected trees that were not excavated by woodpeckers. In such a uniform, middle-aged or old-aged

Sakhalin Fir plantation, decay caused by *P. hartigii* is a more important factor than DBH in explaining woodpecker preferences for nesting and foraging sites. This plantation was kept well and suppressed trees were cut. Thus all of the trees in this plantation were very similar in height, age, slope of ground, and so on, as in an experiment. As a consequence of this, it was practical to isolate just the two variables DBH and fungal infection. Although a multivariate approach is beneficial in evaluating habitat quality (Swallow et al. 1988), a simple approach, where natural habitat variation is lacking such as in this study, is also useful.

Most of the excavations in the study area were likely to have been made by Great Spotted and Japanese Pygmy woodpeckers as these were the only common species observed there. Although the Japanese Pygmy Woodpecker is smaller, and a weaker excavator than the Great Spotted Woodpecker, I have often seen Japanese Pygmy Woodpeckers foraging on large Sakhalin Fir trunks infected with *P. hartigii*. Although Matsuoka (1979) reported that Great Spotted woodpeckers generally forage on thicker parts of trees than Japanese Pygmy Woodpeckers in broad-leaved forest, these two woodpecker species may have very similar preferences in Sakhalin Fir tree size when these are infected by *P. hartigii*.

It is assumed that Sakhalin Fir trees become infected with *P. hartigii* spores carried by wind from its fruiting bodies (Division of forest protection Hokkaido branch FFPRI 1985). But there have been no reports indicating that infection spreads through plantations as a result of leaving infected trees intact. Furthermore the germinability of *P. hartigii*'s spores is weak (M. Akimoto personal communication). Thus leaving a moderate number of trees infected by *P. hartigii* in Sakhalin Fir plantations may not be problematic for either the trees or foresters, but will help woodpeckers. In order to improve the attractiveness of Sakhalin Fir plantations for woodpeckers, some trees infected with *P. hartigii* should be left when the plantations are thinned-out or felled.

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SHORT COMMUNICATION

A new breeding tactic of the Common Moorhen: interspecific brood parasitism of bittern nests

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In a large number of bird species, some females take a reproductive shortcut by laying eggs in the nests of conspecifics (Yom-Tov 1980). Intraspecific brood parasitism is common in some species of water birds, e.g. ducks (Weller 1959), the Common Moorhen *Gallinula c. chloropus* (Gibbons 1986; McRae 1995; McRae & Burke 1996) and the American Coot *Fulica americana* (Lyon 1993a, b). Among water birds, the moorhen is a well-studied species in which intraspecific brood parasitism occurs; at least 10% of nests received parasitic eggs in England for example (McRae 1995), and intraspecific brood parasitism has also been reported from Japan (Ueda et al. 1993). However, interspecific brood parasitism has not previously been documented in the moorhen.

In the course of a three-year study of the breeding ecology of the Chinese Little Bittern *Ixobrychus sinensis* at Akigase, Japan, parasitism of a Chinese Little Bittern nest by a moorhen was noted—the first record of interspecific brood parasitism in this species (Ueda 1993). Since that finding, however, there have been no further reports of interspecific brood parasitism in the moorhen, thus it was not clear whether interspecific brood parasitism is a regular aspect of the moorhen's breeding system or not. Seven years after the first finding we recommenced a study of the breeding ecology of the Chinese Little Bittern at the same site in 2000, and found interspecific brood parasitism by the moorhen again, indicating that interspecific brood parasitism is not rare, at least in this local moorhen population. We discuss the potential causes of this unique behavioural trait.

STUDY AREA AND METHODS

Fieldwork was conducted during five breeding sea-

sons (1991–93 and 2000–2001). The study area was the Akigase paddy field in Saitama Prefecture, 30 km north of Tokyo (35°50'N, 139°37'E). This 47.2 ha paddy field consists of scattered grasslands, cattail swamps, ponds and reed beds. Many marsh nesting bird species, including the moorhen, nest in this area (e.g. Chinese Little Bittern, Spot-billed Duck *Anas poecilorhyncha*, Ruddy Crake *Porzana fusca*, Painted Snipe *Rostratula benghalensis*, Eastern Great Reed Warbler *Acrocephalus orientalis*, and Black-browed Reed Warbler *A. bistrigiceps*). We searched for Chinese Little Bittern nests in the study area; especially, intensive searches were conducted in a small cattail *Typha angustata* swamp (ca. 920m²) at the center of the study area. Once a Chinese Little Bittern nest had been located we checked its contents daily, or every two days, to determine the clutch size and the sequence of eggs laid. Each egg was marked on the day when it was laid, enabling us to detect egg parasitism in a nest.

RESULTS

A total of 150 Chinese Little Bittern nests were found in the study area in 1991–93 and in 2000–2001 (Table 1). Of these bittern nests, three (2.0%) were parasitized by moorhens: one in 1993, and two in 2000. The rate of parasitism, both in 1993 and 2000, was the same at 4.2%. All three parasitized nests were found in a swamp where the nest density of the Chinese Little Bittern was very high (e.g. 21 nests in a 30×30 swamp in 1992). As about half of the bittern nests were found in this cattail swamp every year, if the rate of parasitism in this area alone is calculated, then the rate of parasitism was 7.1% in 1993 and 8.7% in 2000.

The first known case of interspecific brood parasitism involving a moorhen laying its egg in a yellow bittern's nest occurred in the same cattail swamp in

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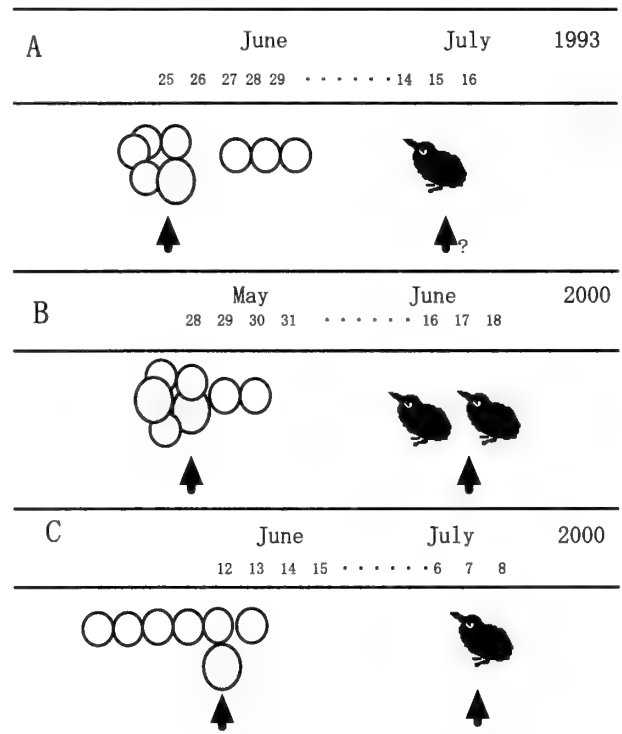
Table 1. Frequency of parasitized nests of Chinese Little Bitterns. Figures in parentheses indicate rates of parasitism.

	No. of bittern nests	
	found	parasitized (%)
1991	25	0
1992	29	0
1993	24	1 (4.2)
2000	48	2 (4.2)
2001	24	0
Total	150	3 (2.0)

1993. In that incident, a bittern nest (A) was found on 25 June 1993 (Ueda pers. obs.), this was during the egg laying stage and the nest contained four bittern eggs and one moorhen egg (Fig. 1). A moorhen nest containing 11 eggs was also found within one meter of the bittern's nest. The number of eggs in the bittern nest had not increased the following day, however, some traces of yolk were found on the eggs in the nest. The bittern laid its 5th, 6th and 7th eggs on 27, 28 and 29 June, respectively, thereby completing its clutch. During the same period four more eggs were also added in the adjacent moorhen nest. The breeding stages of both nests progressed synchronously.

On 14 July 1993, hatching had begun in the bittern nest containing the single moorhen egg. When the nest was next checked, on the morning of 16 July, six Chinese Little Bittern chicks were sitting on the nest and one unhatched bittern egg remained, but there was no sign of the moorhen egg. We judged that the moorhen egg had hatched on 15 July and the chick had already left the nest, because moorhen hatchlings immediately leave the nest within the day of hatching (personal observation of other moorhen nests). At the neighbouring moorhen nest, hatching also begun on the day.

The second record of interspecific brood parasitism was found in the same swamp seven years after the first (Narui pers. obs.). A bittern nest (B) containing three bittern eggs and two moorhen eggs was found on 28 May 2000 (Fig. 1). Both of the moorhen eggs were similar in shape and color pattern, indicating that they had probably been laid by a single female. One bittern egg was added to the clutch on 29 May, but two bittern eggs disappeared from the nest the following day. The fifth egg was laid on 31 May. An active moorhen nest was found within 2 m of the bittern nest, and at the same breeding stage as the bittern

**Fig. 1.** Chronology of moorhen parasitism of Chinese Little Bittern nests found in 1993 and 2000. Small open circles represent bittern eggs and large shaded circles are the moorhen's. Arrows indicate the day on which the moorhen egg was laid or hatched.

nest. We inspected the nest contents regularly during the incubation period. On 16 June, the first Chinese Little Bittern chick hatched, then on the following morning, 17 June, two moorhen eggs and two bittern eggs also hatched (Fig. 2). During the day three bittern chicks and two moorhen chicks were found sitting on the nest, however, when the nest was inspected again on 18 May only the three bittern chicks remained on the nest, and the moorhen chicks were missing.

The third incident was noted in the same swamp on 12 June 2000 (Narui pers. obs.) (Fig. 1). One moorhen egg was added to bittern nest C on the date on which the bittern laid its 5th egg (also the first day of incubation). The last bittern egg was laid the following day (13 June). The bittern eggs hatched successively on 30 June, 1 and 2 July, whereas the moorhen egg hatched on 3 July and the chick left the nest the same day. In this case too an active moorhen nest, also at the incubation stage, was found within 2 m of the bittern's nest.



Fig. 2. A moorhen chick (under the white arrow) with its nest mates in a yellow bittern nest.

DISCUSSION

Interspecific brood parasitism is common in a large number of birds, for example, cuckoos and cowbirds (Anderson 1984; Davies 2000). In waterfowl interspecific brood parasitism is also common. Many duck species lay their eggs in other birds' nests in North America (Weller 1959, 1968). The Black-headed Duck *Heteronetta atricapilla* of South America is a famous specialist nest parasite, never caring for its own eggs or chicks and instead parasitizing another duck, the Rosy-billed Pochard *Netta peposaca*, two species of coots *Fulica* spp. and several other hosts, including gulls *Larus* spp. and ibises *Eudocimus* spp. (Weller 1968). Interspecific brood parasitism occurs occasionally in other duck species in North America (Weller 1959). The Redhead *Aythya americana* for example typically constructs its own nest; however, sometimes it lays eggs in the nests of northern Pintail *Anas acuta*, Mallard *A. platyrhynchos*, Cinnamon Teal *A. cyanoptera*, Ruddy Duck *Oxyura jamaicensis*, Canvasback *Aythya valisineria* and occasionally even in the nests of American Coot and American Bittern *Botaurus lentiginosus*. Furthermore, rails *Rallus* spp. and even the Common Pheasant *Phasianus colchicus* had been reported as occasionally being parasitized by certain ducks (Weller 1959). However, there has been no report of interspecific brood parasitism by members of the Rallidae (rails, coots, and moorhens).

In general, the cost of parasitism is quite low for

bitterns, because moorhen chicks require no parental care from the host once incubation is complete. Immediately after hatching moorhen chicks leave their nest. Thus the cost to the bitterns of moorhen parasitism involves only the cost of incubating one or two additional eggs, assuming, that is, that the moorhen does not remove host eggs, as certain other brood parasites do, such as the Common Cuckoo *Cuculus canorus*. In this study, we found no evidence of egg removal by moorhens. Moorhen eggs were successfully incubated and hatched, as were the bitterns'. No mortality was observed within the bittern clutch, indicating that incubating parasitic eggs was not a significant cost to the host parents.

The potential problem arising in such cases of brood parasitism is the survival of the moorhen chicks after they leave the bittern nest. Moorhen chicks require some parental care prior to their independence. This problem was avoided by the close proximity of a moorhen nest (presumably that of the parasitic egg-layer) to the host nest in each of the three cases recorded here. The moorhen is a precocial species in which the chicks are able to walk within one day of hatching. The moorhen chicks were thus able to leave their host nest and join a group of chicks (probably their siblings) from the nearby conspecific nest. In all three of these cases, all of the moorhen eggs hatched successfully and the chicks seemed to leave the host nest. It appears then that such interspecific brood parasitism is neither wasteful nor maladaptive in this local moorhen population, and it can

be regarded as an alternative breeding tactic in the moorhen.

There are certain prerequisites for the occurrence of a host-parasite relationship between the moorhen and the bittern; these include their temporal and spatial coexistence. The distribution of both species overlaps completely in the four main islands of Japan from Kyushu to Hokkaido (OSJ 2000). Their nesting habitat also completely overlaps, in that they both prefer lowland marshes and swamps for nesting in. The moorhen commences nesting in April and its breeding season extends into October, whereas the breeding season of the Chinese Little Bittern is slightly shorter, commencing in late May and ceasing by the end of August, nevertheless its breeding season completely coincides with that of the moorhen.

Their breeding phenology are also similar: the incubation period of the Chinese Little Bittern, reported as 22 days by Hancock and Kushlan (1984), was found to be 17 to 20 days ($18.7 \pm 1.2 (\bar{x} \pm SD)$ days in average) in Saitama Prefecture, Japan (Uchida & Matsuda 1990), what that of the moorhen is also 17 to 22 days (Harrison 1975; Taylor 1996). The timing of laying of parasitic moorhen eggs is coincident with that of egg laying by the bitterns. Such synchrony between these species suggests that their host-parasite relationship may not be accidental, but may be regular.

The breeding system of the common moorhen is very complicated. In addition to inter- and intra-specific brood parasitism, cooperative breeding and polygamous matings have also been described from populations in England and are to be expected in the Japanese population (Gibbons 1986; McRae 1995; McRae & Burke 1996). More detailed studies of the breeding behaviour of the common moorhen are needed to determine which females in a population parasitize host nests and to clarify the evolutionary causes of such interspecific brood parasitism.

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CONTENTS OF VOLUME 3

Number 1 January 2004

SPECIAL FEATURE

Invasive bird species

Sodhi NS & Eguchi K

Introduction

1

Eguchi K & Amano HE

Spread of exotic birds in Japan

3

Kawakami K & Yamaguchi Y

The spread of the introduced Melodious

Laughing Thrush *Garrulax canorus* in Japan

13

Tojo H & Nakamura S

Breeding density of exotic Red-billed Leiothrix
and native bird species on Mt. Tsukuba,
central Japan

23

Brook BW

Australasian bird invasions: accidents of
history?

33

Leven MR & Corlett RT

Invasive birds in Hong Kong, China

43

Yap CAM & Sodhi NS

Southeast Asian invasive birds: ecology,
impact and management

57

ORIGINAL ARTICLES

Nakamura M & Murayama S

Are Carrion Crows that congregate in spring
roosts juveniles or adults?

69

Paszkowski CA, Sodhi NS, Jamieson S & Zohar SA

Habitat use and foraging behavior of male Black-and-white Warblers (*Mniotilta varia*) in forest fragments and in a contiguous boreal forest 75

Yamazaki Y, Yamada H, Murofushi M, Momose H & Okanoya K

Estimation of hearing range in raptors using unconditioned responses 85

A List of Referees 2003 93

Abstracts of the Japanese Journal of Ornithology, Volume 52 93

Number 2 October 2004

ORIGINAL ARTICLES

Poonswad P, Tsuji A & Jirawatkavi N

Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand 99

Sharma RC, Bhatt D & Sharma RK

Breeding success of the tropical Spotted Munia *Lonchura punctulata* in urbanized and forest habitats 113

Swennen C & Yu Y-t

Notes on feeding structures of the Black-faced Spoonbill *Platalea minor* 119

Chiba A

Microscopic structure and distribution of various elements in the eggshell of the Black-tailed Gull, *Larus crassirostris*, as revealed by scanning and transmission electron microscopy and X-ray compositional microanalysis 125

Pruett CL, Gibson DD & Winker K

Amak Island Song Sparrows (*Melospiza melodia amaka*) are not evolutionarily significant 133

Raju AJS & Rao SP

Passerine bird pollination and fruiting behaviour in a dry season blooming tree species, *Erythrina suberosa* Roxb. (Fabaceae) in the Eastern Ghats forests, India 139

Warkentin IG, Reed JM & Dunham SM

Offspring size as an index of habitat degradation 145

SHORT COMMUNICATIONS

Kawakami K & Fujita M

Feral cat predation on seabirds on Hahajima, the Bonin Islands, Southern Japan 155

Unno A

The effect of the fungus *Phellinus hartigii* on woodpecker habitat quality in Hokkaido, Japan 159

Ueda K & Narui Y

A new breeding tactic of the common moorhan: interspecific brood parasitism of bittern nests 163

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ORNITHOLOGICAL SCIENCE

Volume 3 Number 2 October 2004

Contents

ORIGINAL ARTICLES

Poonswad P, Tsuji A & Jirawatkavi N

Estimation of nutrients delivered to nest inmates by four sympatric species of hornbills in Khao Yai National Park, Thailand 99

Sharma RC, Bhatt D & Sharma RK

Breeding success of the tropical Spotted Munia *Lonchura punctulata* in urbanized and forest habitats 113

Swennen C & Yu Y-t

Notes on feeding structures of the Black-faced Spoonbill *Platalea minor* 119

Chiba A

Microscopic structure and distribution of various elements in the eggshell of the Black-tailed Gull, *Larus crassirostris*, as revealed by scanning and transmission electron microscopy and X-ray compositional microanalysis 125

Pruett CL, Gibson DD & Winker K

Amak Island Song Sparrows (*Melospiza melodia amaka*) are not evolutionarily significant 133

Raju AJS & Rao SP

Passerine bird pollination and fruiting behaviour in a dry season blooming tree species, *Erythrina suberosa* Roxb. (Fabaceae) in the Eastern Ghats forests, India 139

Warkentin IG, Reed JM & Dunham SM

Offspring size as an index of habitat degradation 145

SHORT COMMUNICATIONS

Kawakami K & Fujita M

Feral cat predation on seabirds on Hahajima, the Bonin Islands, Southern Japan 155

Unno A

The effect of the fungus *Phellinus hartigii* on woodpecker habitat quality in Hokkaido, Japan 159

Ueda K & Narui Y

A new breeding tactic of the Common Moorhen: interspecific brood parasitism of bittern nests 163